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EXECUTIVE SUMMARY

This report describes research conducted on vertebrate species of concern inhabiting the longleaf pine ecosystem on Eglin Air Force Base, Florida, during January 2001 through December 2005. This work was conducted first through Research Work Order Number 68 of the USGS-BRD Virginia Cooperative Fish and Wildlife Research Unit at Virginia Tech, and subsequently through a contract awarded through Fort Detrick, U.S. Army Medical Research and Materiel Command.

The research reported here represents a five-year study that had three components: (1) assessment of the success of a new base-wide management strategy for red-cockaded woodpeckers (RCWs); (2) an experimental study of interactions of RCWs with other members of the cavity-nesting bird community; and (3) population studies of bog frogs and flatwoods salamanders. The project also supported graduate student training.

Assessment of RCW Management

The base-wide management strategy employed was based on our previous landscape level experiment in which we tested the cost effectiveness, in terms of stimulating RCW population growth, of management regimes of different intensities. The strategy involved dividing the RCW population into eastern and western subpopulations that were managed in different ways and had different management objectives. At the outset of the study the eastern subpopulation contained 52 active clusters and was considered unstable, whereas the western subpopulation contained 249 active clusters and was considered stable (Figure 1). The recovery goal for the western subpopulation is to increase its size to 250 groups, to be achieved through an annual growth rate of 4%. The recovery goal for the eastern subpopulation is to increase it size to 100 groups, to be achieved through an annual growth rate of 10%. The components of the management strategy for the western subpopulation were ecosystem management, recruitment cluster construction and cavity management. The more intense level of management applied to the eastern subpopulation included these elements plus an additional one, translocation. In this study we assisted Jackson Guard in applying the base-wide management strategy and measured the response of the two subpopulations in terms of population growth.

Over the five years of the study the RCW population grew by 6.7%, from 301 active clusters in 2000 to 321 in 2005 (Figure 2). This represents an annual growth rate of 1.3%. The eastern subpopulation increased more (9.6% or 1.9% per year, from 52 to 57 active clusters) (Figure 3) than the western subpopulation (6.0% or 1.2% per year, from 249 to 264 active clusters) (Figure 4). These increases are far below the objectives of 10% annual growth for the eastern subpopulation and 4% annual growth for the western subpopulation. Annual estimates of the number of RCW groups indicated comparable population growth (Figure 5).

The natural processes of new territory formation of budding and pioneering produced eight active clusters over the course of the study, which translates into a population growth rate of 0.05% per year (Figure 6). This is lower than typical rates of pioneering and budding (1-2% per year), but low rates were expected because of the widespread availability of recruitment clusters, which provide breeding opportunities for young birds that might otherwise initiate budding or pioneering (Table 1). Recruitment cluster construction stimulated population growth as expected, adding 59 active clusters to the population (Figure 6), but these gains were compromised by higher than expected rates of

cluster abandonment (Table 1). Based on our previous study, we set performance objectives of 75% probability of occupancy of recruitment clusters within three years of construction, and an annual occupancy rate of 30% of available recruitment clusters. These performance objectives were achieved: 71% of newly constructed recruitment clusters were occupied within three years, and the annual probability of occupancy was 39% (Figure 9). Although recruitment clusters were as effective at attracting birds as previously, they were not as effective at retaining these birds. Whereas previously abandonment and reoccupation of recruitment clusters were balanced, during the current study abandonment exceeded reoccupation, resulting in a net loss of 11active clusters (Figure 6). More significantly, there was a similar imbalance between abandonment and reoccupation of previously existing clusters, which resulted in a net loss of 35 active clusters over the course of the study (Figure 6).

Based on the management strategy employed and the results of our previous study, we expected group sizes to remain stable on the donor plots from which birds are drawn for translocation and to increase slightly elsewhere. Instead, group sizes in the donor plots declined and elsewhere they remained stable (Figure 7). Productivity was relatively poor during the study, averaging 1.34 fledglings per potential breeding group (2000-2005), compared to 1.47 fledglings per potential breeding group the previous four years. Productivity was particularly poor in 2000 and 2002, perhaps due to drought conditions, but was very high in 2005 (Table 2). Poor productivity likely contributed to lower than expected group sizes. Breeder male retention, an indicator of survival rates, was the same during this study and our previous one (Figure 8). Overall demographic conditions were somewhat unfavorable for population growth because poor productivity reduced the sizes of the nonbreeder classes (fledgling, helper, floater). This may have contributed to poorer than expected growth, especially in the first years of the study, but is not sufficient to explain it.

Another factor contributing to poor population growth in the eastern subpopulation was our inability to effectively implement one component of the management strategy, translocation. With the addition of a second donor plot, we expected there would be 10-12 birds available for translocation each year, half of which would be donated to regional translocation efforts in fall, leaving 5-6 birds for within population translocation in winter. However, we could locate only 3-5 birds eligible for translocation during the last three years of the study, despite adding a third donor plot in 2004 (Table 3). Growth of the eastern subpopulation was reasonable during the first two years of the study, but ceased once the translocation program failed (Figure 3). Demographic data indicate that the paucity of available birds on the donor plots was due either to high mortality or high rates of dispersal of fledgling and helper males (Table 4; Table 5). We think the former is unlikely, whereas construction of recruitment clusters can account for elevated dispersal rates, as well as the declines in group size observed on the donor plots. It may be necessary to refrain from constructing recruitment clusters in donor plots to avoid drawing the "excess" birds that can be used for translocation away from their natal group.

Qualitatively it is clear that Eglin's ecosystem management has greatly improved nesting and foraging habitat for RCWs, reducing hardwood midstory and producing a richer, more diverse groundcover on tens of thousands of acres, and reducing sand pine intrusion in some areas. Ecosystem management has had one unintentional negative impact on RCWs, mortality of cavity trees and other old growth pines during prescribed

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fires. This may have contributed to another deficiency in executing the management strategy, failure to implement cavity management as effectively as planned. Based on our previous study, we anticipated that the proportion of active clusters needing additional cavities each year would stabilize at 8%. Because cavity management was applied base-wide for the first time at the outset of the study, many clusters required cavity management initially. By the third year of the study these initial deficiencies had been addressed and the 8% level was reached (Table 6). However, the next year (2004) many cavities were lost to two hurricanes, greatly increasing the amount of cavity management required. We were not able to fully "catch up" with these losses through cavity management until 2005.

Cavity management is designed to prevent cluster abandonment. There is a lag time between the point at which clusters become deficient in cavity number and the point at which the deficiency is corrected, but this is only a problem when the deficiency is so severe (i.e., only 0-1 good cavities remain) that it creates an imminent threat of abandonment. As long as the number of clusters requiring treatment is low, i.e. under 10%, the minority of cases that result in abandonment prior to treatment can be balanced by reoccupation after treatment. But during this study the proportion of clusters requiring treatment exceeded 10% in four of the five years (Table 6), indicating that cavity losses were exceeding the capacity of cavity management to address them much of the time. We believe that this is the primary cause of the unexpectedly high rate of territory abandonment, and that this high rate of territory abandonment was the primary cause of lower than expected growth of the western subpopulation, and one of the two primary causes, along with the failure of the translocation program, of lower than expected growth of the eastern subpopulation. To keep cavity management activity at a level where it can be effective and reduce territory abandonment in the future, it is necessary to address the two sources of cavity tree loss that can create severe cavity deficiencies in a cluster, hurricanes and fire. We recommend emergency management in response to hurricane losses, and making every effort to reduce losses of cavity trees to prescribed fire. The hurricane response policy Eglin now has in place – to immediately install insert boxes in clusters where cavity tree losses are severe – addresses the first recommendation. There is evidence (declining pine snag densities, Table 13) that improved burning techniques and more effective protection of cavity trees during burns already is reducing mortality due to prescribed fire. Closer inspection of inactive cavities counted as suitable may improve the cavity management procedure.

Despite disappointingly low rates of population growth during the study, Eglin's RCW population remains headed toward recovery, and there is reason for optimism. The spatial aggregation of territories in the eastern subpopulation has been improved (Figure 10). Demographic conditions were more conducive to population growth at the end of the study than at any other point during the study, suggesting that population growth rates may improve in the next few years. The problems in implementing the management strategy we have identified as causes of poor population growth either are being addressed already (cavity management) or can readily be corrected (translocation). We believe that with the slight adjustments in management strategy we suggest higher rates of population growth will be achieved and progress toward recovery will be accelerated.

Experimental Study of the Cavity-nesting Community

Being both stewards of the ecosystem and responsible for recovery of the endangered RCW, Eglin managers must be concerned about possible conflicts between ecosystem management and single-species management. Providing additional cavities for RCWs through cavity management and recruitment cluster construction may benefit other cavity users, but restricting cavities so that larger species cannot use them may have negative effects on some species. We applied methods traditionally used to study food webs to the "nest webs" of the cavity-nesting community in order to characterize the links of the RCW with other members of the cavity-nesting community. RCWs may have numerous and strong links with other cavity-nesting species because only they excavate cavities in live pine trees, and within the fire-maintained longleaf system the snags and hardwoods in which other species excavate cavities are not always widely available.

We established 36, 800x600-meter plots in areas of variable RCW density (Figure 11; Figure 12), and measured the abundance and nest cavity use of members of the cavity-nesting community on these plots, as well as numbers of RCWs, cavities excavated by RCWs, and snags. We also recorded abundance of non-cavity nesters and found that neither species associated with open pine habitat nor species associated with hardwoods were significantly correlated with RCW cavities or with hardwood snags, whereas both groups were positively correlated with pine snags. These results indicate that habitat quality is not confounded with cavity resource availability in our data.

We detected 52 bird species in our censuses, including 14 cavity-nesters that breed on Eglin (Table 8), and found 867 nests of these cavity-nesting species (Table 11). The majority of nests were found in pine snags (59%). The second most common resource used by cavity nesters was the living RCW cavity tree (27%), followed by hardwood snags (10%) and then dead RCW cavity trees (5%). These numbers are heavily influenced by the red-headed woodpecker, which was the most abundant cavity nester detected in this study (36% of nests found) and used, almost exclusively, barkless pine snags.

We identified two nest webs into which most of the cavity-nesting species on Eglin can be placed. One web contains the RCW, red-headed woodpecker, northern flicker, brown-headed nuthatch, southeastern American kestrel and eastern screech owl, which are associated with pine snags and RCW cavities in live pines (Figure 15; Figure 18). The second web contains the eastern tufted titmouse, Carolina chickadee, red-bellied woodpecker, downy woodpecker and great-crested flycatcher, which are associated with hardwood snags. One species, the red-bellied woodpecker, is positively correlated to both pine and hardwood snags and thus connects the hardwood and pine webs. The RCW and northern flicker provided the most cavities used by other species (Figure 16; Figure 17). The northern flicker was the primary creator of large cavities, which are required for nesting by larger secondary cavity-nesters such as the southeastern American kestrel and eastern screech owl. The red-headed woodpecker was the most prolific cavity excavator, but use of its cavities by other species was rare. Our observational work suggests that the RCW can indirectly and positively affect other members of the pine web through its cavity excavation, mediated by the northern flicker in the case of larger species.

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We further examined the relationships revealed by our observational study by experimentally manipulating the availability of normal-sized and enlarged RCW cavities through cavity drilling and application of cavity restrictors. We selected 11 plots for cavity addition and designated 11 additional plots as controls. In a different set of 8 plots we placed restrictors on all inactive and/or enlarged RCW cavities to reduce their availability; we designated 8 control plots for this experiment. The experimental analysis compares 2003 data (pre-treatment) and 2005 data (post-treatment). There was a significantly greater increase in both abundance and number of nests of RCWs on the experimental plots to which cavities were added compared to control plots (Figure 20; Figure 21). Abundance of two other members of the pine web, the red-headed woodpecker and southeastern American kestrel, exhibited a similar response, although the trend was only marginally significant in the case of the kestrel (Table 16). Following application of cavity restrictors, there was a reduction in the number of nests of large secondary cavity-nesters in RCW cavities (Figure 23) and an increase in such nests in snags (Figure 24) on the experimental plots, whereas snag nests of large secondary cavity-nesters decreased on control plots.

The experiments provided some evidence of strong interactions of RCWs with other members of the pine web, but results, being based on only one year of observation post-treatment, were equivocal in some cases. Larger responses to the treatments may occur eventually, and to evaluate this possibility we recommend resampling the plots in 2010. The restrictor experiment suggests that the use of metal restrictor plates on RCW cavities can have negative impacts on large cavity nesters, but these impacts may be mitigated by the availability of large pine snags. Of particular significance is the southeastern American kestrel, a species of concern itself, which appears to have a strong link to the RCW. We recommend that restrictor plates be used sparingly and in combination with retention of large pine snags on the landscape in order to provide for not only southeastern American kestrels, but also the eastern screech owl. Large pine snags are an important nesting resource for cavity-nesting birds on Eglin, and their retention may reduce usurpation of RCW cavities by providing alternate nesting sites for other cavity-nesting species. We recorded much less use of active RCW cavities by some members of the pine web, notably the red-headed woodpecker, than has been reported in other locations where large pine snags are much scarcer. The cavity addition experiment revealed no negative impacts on any other species of providing artificial cavities for RCWs, and positive impacts on some members of the pine web.

It is surprising that the northern flicker, known to be a source of cavities for large secondary cavity-nesters in other ecosystems, fills this same role in Eglin's longleaf ecosystem. That the pileated woodpecker does not play this role is equally surprising, considering that in other locations pileated woodpeckers enlarge many RCW cavities, often severely damaging them.

Large pine snags are abundant on Eglin, their densities greatly exceeding the recommended guidelines proposed for Florida (Table 13). In this respect Eglin is nearly unique among longleaf pine communities today. Documenting the role of these snags in and importance to the cavity-nesting bird community is one of the most important results of our study. The dynamics of the cavity-nesting bird community on Eglin can be used as a baseline for comparison to communities elsewhere where the absence of large, old-

growth snags imposes stress on the relationships between species and presumably increases competition between them.

Population Studies of Amphibians

Eglin is home to a diverse suite of amphibians and reptiles including the federally threatened flatwoods salamander and the recently discovered, endemic Florida bog frog. We collected data on distribution and habitat requirements of these two species in order to improve Eglin's ability to manage for them. In particular our goal was to evaluate current distribution, population size, and turnover of Florida bog frogs, and for flatwoods salamanders, to assess the effects of surrounding land use characteristics on larval density in ponds and collect more detailed demographic information in a few ponds. Much of this work was conducted by David Bishop as part of his Ph.D. dissertation research, and is described in detail in the dissertation and a 2004 report, both of which were previously submitted to Eglin. Here we provide only a summary of this work, reporting full details only for those aspects of the work not described in these other documents.

We conducted surveys for larval salamanders via dip-netting in wetlands identified by the Florida Natural Areas Inventory (FNAI) as active or potential breeding wetlands, and in additional wetlands that we identified as potential habitat. Surveys were conducted at 105 of the 110 wetlands on Eglin considered to have some potential as breeding sites, 58 of which we determined were too ephemeral or surrounded by habitat too xeric for them to serve as breeding ponds. Prior to this study flatwoods salamanders had been documented in 17 wetlands on Eglin, and we detected salamanders at six of these historic breeding locations and one new location (Table 18). At only one location were salamanders detected in all three years of sampling, and they were detected in only one year at three of the seven sites. Many of the 17 historic sites never contained sufficient water to be sampled during the study period. Thus flatwoods salamanders have now been captured at 18 different wetlands on Eglin, but they have not been recorded at several of these sites for over a decade. There likely was little population recruitment over the last few years, even from the few wetlands where larvae were detected. It is difficult to determine the extent to which our observations indicate a population decline rather than reduced activity due to poor breeding conditions brought about by drought. Drift fence sampling and roadside surveys for adults proved inefficient due to extremely low encounter rates, precluding us from assessing adult demography or population size.

We assessed effects of fire on wetlands used by flatwoods salamanders by collecting data on water chemistry and habitat characteristics of 13 ponds and relating these features to burn history. Recently burned wetlands had more open canopies, higher dissolved oxygen concentrations, higher water temperatures, more understory vegetation, and lower water depths than unburned areas. These impacts of burning likely influence salamander reproduction positively, and therefore we suggest that more frequent burning of wetlands, particularly growing season burning, would improve conditions for the salamanders.

To assess bog frog distribution, in 2002-2005 we surveyed sites identified by FNAI and additional sites with similar habitat for calling adults. Florida bog frogs have been detected at 66 locations, 29 of which are new sites documented during this study (Figure 25). These new locations are located in previously documented drainages. Of the 37 historic sites, 23 were active during at least one year from 2002-2005 (Table 19). We did not visit every site every year, but the 14 historic sites that had no confirmed presence

during 2002-2005 were all visited in at least two years, suggesting that most or all of them are no longer used by the frogs. Repeated visits to sites within a year indicated the probability of detecting frogs in a single visit in a site occupied by bog frogs was 66%. Bog frogs were less likely to call at cool temperatures and early in the season (Figure 27). To track population trends, we recommend focusing on a subset of sites and visiting these repeatedly each year, rather than trying to survey all sites each year.

The general features of Florida bog frog habitat are now clear. Within occupied drainages on Eglin, there are distinct gaps in the distribution of bog frogs, and in some cases the general habitat characteristics of occupied and unoccupied streams are not noticeably different. The same may be said of occupied drainages compared to unoccupied drainages in eastern Eglin. It may be that bog frog distribution is limited by finer details of habitat features than those we assessed. We originally planned to quantify habitat characteristics of surveyed sites in order to compare occupied and unoccupied sites, and thereby better specify the habitat requirements of the species. However, we decided to defer this aspect of the study in order to increase emphasis on studies of frog behavior and demography, which proved surprisingly conducive to study. Habitat selection by Florida bog frogs is a major component of the Ph.D. dissertation research of Tom Gorman, who joined our research team in August 2005, and his work may clarify distribution patterns. It may be that not only habitat requirements, but also dispersal behavior and metapopulation dynamics limit bog frog distribution. That is, the frogs may be absent from suitable habitat in some locations because individuals are unable to access those locations through dispersal from existing populations, or because local populations cycle through periods of extinction and recolonization. Dispersal behavior and metapopulation dynamics are additional aspects of bog frog biology we will pursue in subsequent research.

The behavior, population biology and vocalizations of the Florida bog frog were the focus of David Bishop's research; results for this aspect of the project are fully described in his dissertation.

Graduate Student Training
The project provided funding for two graduate students. One position was occupied by Ms. Lori Blanc, who began her degree program at the outset of the project in January 2001, and thus received five years of funding. The cavity-nester study constitutes Ms. Blanc's Ph.D. dissertation research. Her dissertation will include, in addition to the results presented in this report, path modeling of interactions between cavity-nesting bird species at Eglin, based on cavity resource-use. Ms. Blanc's dissertation will be submitted to Eglin as an additional product of the project when it is completed in May 2007.

The second position initially was occupied by David Bishop, starting in August 2001 when he began his degree program. Dr. Bishop conducted the work on amphibians reported here as his Ph.D. dissertation research. He received four years of funding, and completed his dissertation in June 2005. This dissertation has already been submitted to Eglin as an additional product of the project. Following Dr. Bishop's graduation, the second position was occupied by Mr. Tom Gorman for one semester at the end of the project (August – December 2005). Mr. Gorman is continuing the work on salamanders and frogs begun by Dr. Bishop.

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INTRODUCTION

This report describes research conducted on vertebrate species of concern inhabiting the longleaf pine (*Pinus palustris*) ecosystem on Eglin Air Force Base, Florida, during January 2001 through December 2005. This work was conducted first through a cooperative agreement under Research Work Order Number 68, Biological Resources Division, U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit at Virginia Polytechnic Institute and State University, Department of Fisheries and Wildlife Science, and subsequently through a contract awarded through Fort Detrick, U.S. Army Medical Research and Materiel Command. The report also summarizes graduate training accomplished during the study period.

The research and training reported here represents a five-year study that had three components: (1) assessment of the success of a new base-wide management strategy for red-cockaded woodpeckers (*Picoides borealis*); (2) an experimental study of interactions of red-cockaded woodpeckers with other members of the cavity-nesting bird community; and (3) population studies of bog frogs (*Rana okaloosae*) and flatwoods salamanders (*Ambystoma cingulatum*). We will describe each component in turn, including background, objectives, methods, results and discussion. We will conclude by describing graduate training accomplishments.

ASSESSMENT OF RED-COCKADED WOODPECKER MANAGEMENT
Background

The red-cockaded woodpecker (RCW) is an endangered species endemic to the pine savannas of the southeastern United States. The species has declined due to habitat loss and alteration of remaining habitat, specifically loss of old growth pine and development of hardwood midstory due to fire suppression (Walters 1991; USFWS 2003). It has been extensively studied, for example it has been the subject of four symposia (Thompson 1971; Wood 1983; Kulhavy et al. 1995; Costa and Daniels 2004) and two books (McFarlane 1992; Conner et al. 2001), and its biology is well known (Walters 1990; 1991; Jackson 1994; USFWS 2003).

The population dynamics of the RCW are unusual, and appear to revolve around two linked peculiarities of its biology, (1) its unique habit of constructing its cavities in living pines and (2) its cooperative breeding system (Walters 1991; Conner et al. 2001; Rudolph et al. 2004). Cavities excavated in living pines take years to construct, but can be used for decades (Jackson et al. 1979; Conner and Rudolph 1995; Harding and Walters 2002; 2004), and hence are an extremely valuable resource. Presumably because of this, the birds apparently perceive habitat with existing cavities as high quality, and otherwise suitable habitat lacking cavities as low quality. Individuals generally compete for breeding vacancies on territories with existing cavities rather than move into unoccupied habitat and construct a new set of cavities. Territories with good cavities remain occupied continuously, often for decades (Doerr et al. 1989), whereas rates of new territory formation are extremely low (i.e., 1-2% increase per year) (Hooper et al. 1991; Conner et al. 2001; Walters 2004). New territory formation can occur through budding, in which one group splits into two and divides the existing cavities, or by pioneering, in which birds occupy previously vacant habitat and construct new cavities (Hooper 1983). Budding is by far more common (Conner et al. 2001).

These unusual dynamics suggest that the best management strategy is one that focuses on territory quality, and therefore is devised to prevent abandonment of existing territories and create additional new territories, as opposed to a strategy that focuses on demography, and is devised to increase reproduction or reduce mortality. Such a management strategy, employing a number of special management techniques, has been developed (Walters 1991; Conner et al. 2001; Rudloph et al. 2004). Cavity restrictors (Carter et al. 1989) are designed to reduce territory abandonment by protecting cavities from enlargement. Construction of artificial cavities (Copeyon 1990; Allen 1991; Copeyon et al. 1991) can be used both to maintain territory quality by providing replacement cavities in existing clusters, and to create new territories, called recruitment clusters, by providing cavities in unoccupied habitat. Translocation of juveniles from their natal groups to recruitment clusters is employed to increase the rate of new group formation (and thus population increase) in recruitment clusters (DeFazio et al. 1987; Rudolph et al. 1992; Allen et al. 1993; Edwards and Costa 2004). Growing season fire, herbicides and mechanical removal are used to reduce hardwood midstory that might encroach on cavities, and thereby induce territory abandonment (Frost et al. 1986; Ware et al. 1993; Provencher et al. 2002). Management based on these techniques has been highly successful in stabilizing and even increasing RCW populations (Watson et al. 1995; Franzreb 1997; Conner et al. 2001; Walters 2004), resulting in new optimism about the recovery of the species (Costa 1995; 2004).

In our previous project, we conducted an exercise in adaptive management (Walters and Holling 1990) designed to identify the most cost-effective strategy for managing RCWs on Eglin Air Force Base. Specifically, we performed a landscape-level experiment in which the management techniques described above were applied to replicate plots in various combinations representing different levels of management intensity (Walters et al. 2002a; 2004). The lowest intensity level, ecosystem management, included only those components (i.e., growing season fire and forest management) that benefit the ecosystem generally rather than RCWs specifically. The highest intensity level included not only ecosystem management, but also all the special management techniques for RCWs described above. We measured several response variables, including population growth rate. Population growth was perfectly correlated with management intensity level, and varied from 2% per year in the lowest management intensity treatment, to 12% per year in the highest management intensity treatment.

Using the relationship between management resources expended and population growth achieved in our previous study, in consultation with natural resource managers at Eglin (Jackson Guard) we identified an appropriate base-wide management strategy that was then employed throughout the current study. The woodpecker population on the base was divided into two subpopulations that were managed in different ways and had different management objectives. The eastern subpopulation includes the clusters east of highway 85, the western subpopulation those west of highway 85 (Figure 1). At the outset of the study (i.e., 2000 breeding season) the eastern subpopulation contained 52 active clusters, and was considered unstable because of low population density, a fragmented distribution of groups, and poor connectivity to the larger western subpopulation. The western subpopulation contained 249 active clusters and was considered stable. These characterizations of the status of the two subpopulations are supported by simulation modeling as well as empirical evidence (Crowder et al. 2000).
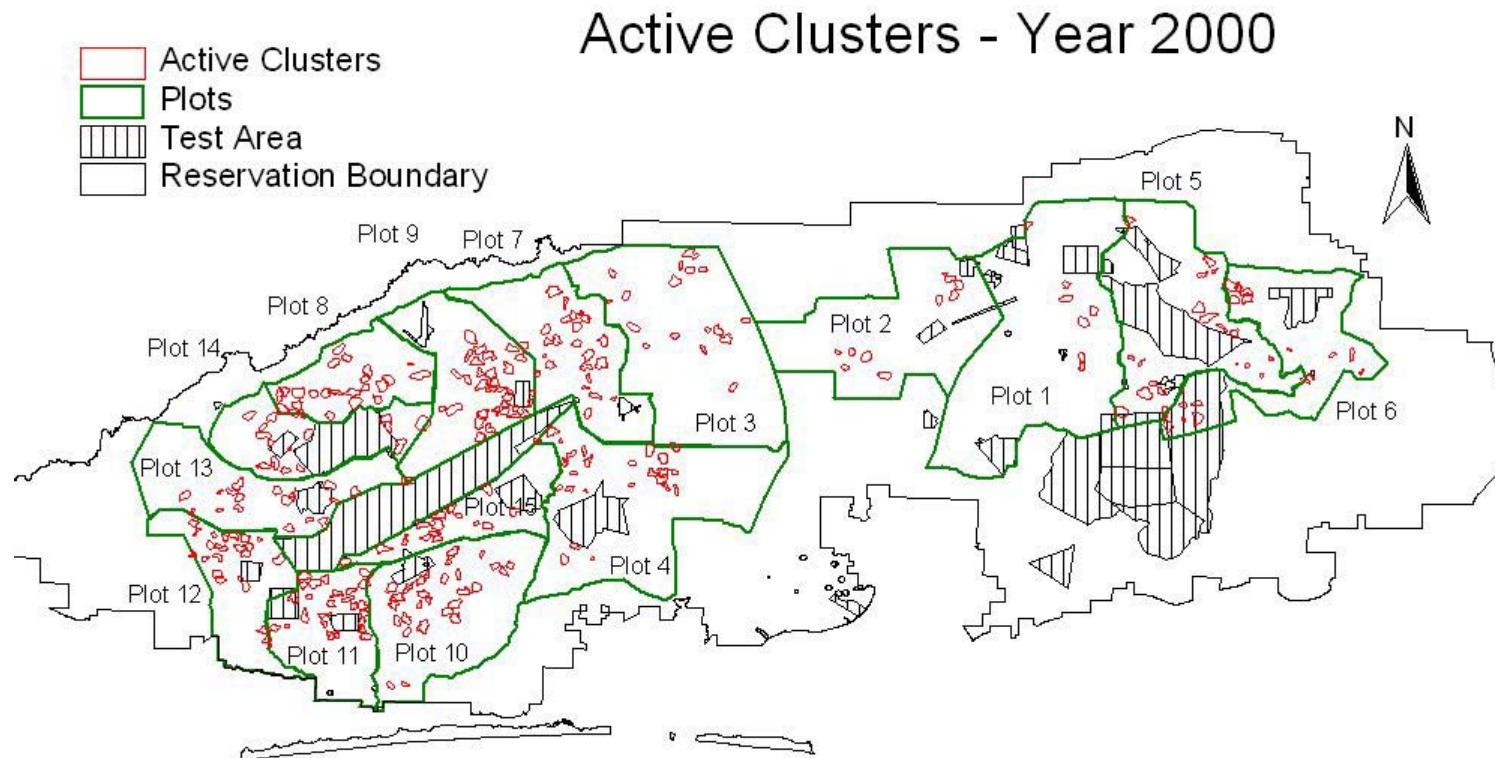
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Figure 1. Active red-cockaded woodpecker clusters on Eglin Air Force Base in 2000. Study plots are indicated by number, and military test ranges that contain some cleared areas are shown (Test Area).

The objective for each subpopulation is to reach its recovery goal, as identified by Jackson Guard. The recovery goal for the western subpopulation is 250 groups, to be achieved through an annual growth rate of 4%. Simulation modeling indicates that well distributed populations of 250 groups are viable demographically (Walters et al. 2002b), and this viability standard is adopted in the new Recovery Plan for the species (USFWS 2003). The recovery goal for the eastern subpopulation is 100 groups, to be achieved through an annual growth rate of 10%. This goal is based on simulation modeling which projects a subpopulation of 100 groups with appropriate spatial distribution to be stable (Crowder et al. 2000). When both subpopulations are recovered, the total population will be at least 350 groups, which is the population size objective mandated for Eglin as a Primary Core Population in the new Recovery Plan (USFWS 2003). The management strategies for each subpopulation are ones that produced population growth rates in excess of the objectives (6% vs. 4% for the western subpopulation, 12% vs. 10% for the eastern subpopulation) in the management experiment.

In this study we assisted Jackson Guard in applying the base-wide management strategy and measured the response of the two subpopulations in terms of population growth. We projected that if population growth objectives were achieved, the recovery goal for the western subpopulation would be reached within the study period, but the recovery goal for the eastern subpopulation would not be. Therefore we did not anticipate attaining recovery of the total population during the study.

Objectives

1. To assist in implementing the base-wide management strategy for red-cockaded woodpeckers on Eglin Air Force Base.
2. To measure annual population growth in terms of the number of active cavity tree clusters and estimated number of potential breeding groups in the eastern and western subpopulations of red-cockaded woodpeckers on Eglin.

Methods

A more intense level of management was applied to the eastern subpopulation than to the western subpopulation. The components of the management strategy for the western subpopulation were ecosystem management, recruitment cluster construction and cavity management. Ecosystem management refers to practices adopted by Eglin to promote longleaf pine ecosystems generally, as well as RCWs specifically. The critical elements are prescribed burning, especially growing season burning, timber management and ecosystem restoration, including removal of hardwood and sand pine (*Pinus clausa*). These practices increase the quantity and quality of RCW habitat. Recruitment cluster construction is a technique designed to benefit RCWs specifically. As applied in this study, it involved drilling sets of four artificial cavities to create new clusters in strategic locations in order to stimulate new group formation, and thus population growth. Cavity management consisted of checking each active cluster each year to determine if sufficient numbers of suitable cavities were present. If there were too few such cavities in a cluster, additional cavities were provided, either by placing cavity restrictors on suitable but enlarged cavities, or drilling new artificial cavities. This practice is designed to prevent cluster abandonment by ensuring that all clusters are of sufficiently high quality.

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The elements of the more intense strategy for the eastern subpopulation included, in addition to ecosystem management, recruitment cluster construction and cavity management, translocation. Translocation involved moving juvenile males and females from groups within the western subpopulation to clusters with unpaired males or unoccupied recruitment clusters in the eastern subpopulation. This procedure was designed to promote population growth by increasing the number of breeding pairs. Juvenile females were moved to unpaired males, and either juvenile males alone or a male – female pair of juveniles to unoccupied clusters.

Jackson Guard conducted ecosystem management activities, while we, with assistance from Jackson Guard, carried out recruitment cluster construction, cavity management and translocation. Initially the number of cavities maintained through cavity management was three, but in 2002 this number was increased to four. The criteria for recruitment cluster construction at the outset of the study were to have four unoccupied recruitment clusters available each year in each of the four plots in the eastern subpopulation, and two clusters in each of the 11 plots in the western subpopulation. These criteria were established in accordance with the different population growth objectives of the eastern and western subpopulations. In the east, placement of new recruitment clusters was designed to reduce territory isolation and increase connectivity to the western subpopulation. In the west, placement of new recruitment clusters was designed to increase connectivity with the eastern subpopulation and to promote growth in areas that are not heavily used for military training. As the study progressed, it became difficult to find additional recruitment cluster locations in some plots. Therefore in 2004 the previous plot-specific criteria were replaced by a new criterion to provide at least 40 unoccupied recruitment clusters base-wide, or a number equal to 10% of the number of active clusters, whichever is larger.

At the beginning of the study two plots in the western subpopulation (7 and 9) containing approximately 50 groups served as the source of juveniles for translocation (donor plots) (Figure 1). We monitored all groups in the donor plots during the breeding season, which involved marking group members with individually-identifiable color band combinations, censusing each group to determine group composition, visiting each cluster weekly to check for nesting activity, banding nestlings, and determining which nestlings fledged. After the breeding season we identified juveniles suitable for translocation according to USFWS (2003) criteria. In 2004, a third plot (8) was converted to a donor plot in order to increase the number of juveniles available for translocation (Figure 1).

In addition to applying these management treatments, we carried out a variety of other activities in order to track the number of active clusters and potential breeding groups in the population. Once occupied, recruitment clusters were monitored during the breeding season to determine whether nesting occurred, but young were not banded and the number of fledglings was not determined. Once nesting occurred in two different years, recruitment clusters were no longer monitored. In addition, we determined breeding season group size in a 20% sample of the active clusters in the western subpopulation and a 25% sample in the eastern subpopulation (monitoring sample). The purpose of this monitoring sampling was to estimate the number of potential breeding groups in the population based on the proportion of active clusters occupied by groups, as opposed to being occupied by unpaired males or captured (i.e., used by members of a

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group whose primary residence is another cluster). The number of active clusters was tracked by direct count based on checks of all clusters on Eglin at the beginning of each breeding season.

Surveys of inactive clusters, surveys for new pioneer clusters and checks of active clusters for budding were conducted on a seven-year cycle, achieved by conducting these activities on 2-3 of the 15 plots on Eglin each year. In inactive cluster surveys, we checked all known cavity trees for activity, and surveyed 160 acres centered on the known cavity trees for new cavity trees. This procedure was designed to detect cluster reactivation and shifts in cluster location. In bud checks, we censused the group and surveyed 160 acres centered on the known active cavity trees to determine whether the group had split. In pioneer surveys, we searched suitable habitat outside of known clusters and inactive check and bud check survey areas for new cavity trees. This procedure was designed to detect new groups that formed by pioneering.

We assessed success of the base-wide management strategy in terms of ability to reach the population growth objectives of 4% annual growth in the western subpopulation and 10% annual growth in the eastern subpopulation.

Results and Discussion

Population Growth

The most reliable indicator of population size is the number of active clusters, because it is based on a complete count rather than an estimate. By this measure, the RCW population on Eglin Air Force Base grew by 6.7% over the five years of the study, from 301 active clusters in 2000 to 321 in 2005 (Figure 2). This represents an annual growth rate of 1.3%. Under the more intense management regime, the eastern subpopulation increased more (9.6% or 1.9% per year, from 52 to 57 active clusters) (Figure 3) than the western subpopulation (6.0% or 1.2% per year, from 249 to 264 active clusters) (Figure 4). These increases are far below the objectives of 10% annual growth for the eastern subpopulation and 4% annual growth for the western subpopulation, which if achieved would have resulted in 84 active clusters in the eastern subpopulation and 364 active clusters in the western subpopulation, for a total population of 448 active clusters by 2005, compared to the actual population of 321 active clusters.
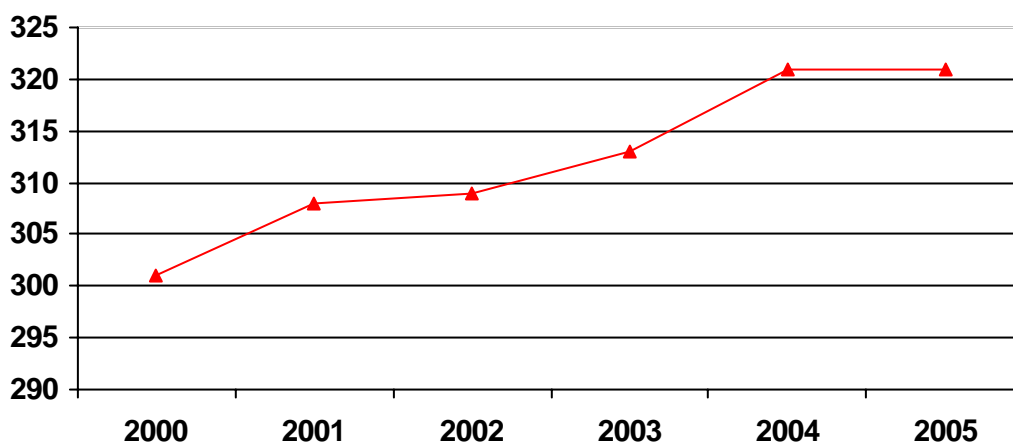
Figure 2. Number of active RCW clusters on Eglin Air Force Base, 2000-2005.

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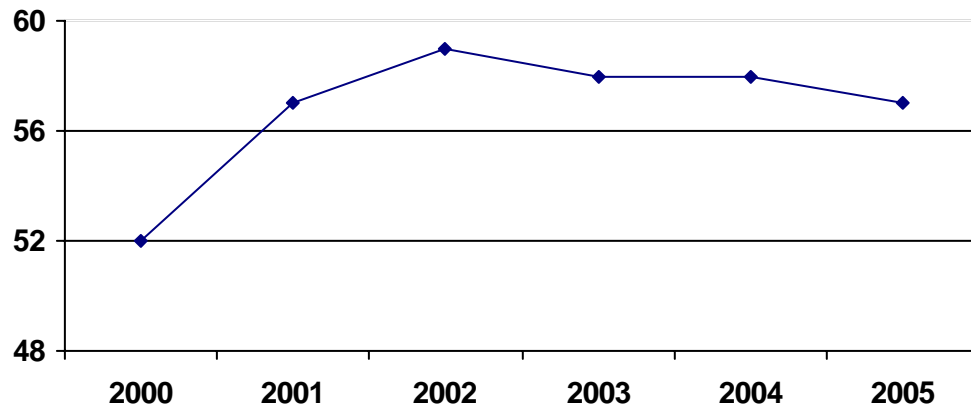
Figure 3. Number of active RCW clusters in the eastern subpopulation, 2000-2005.
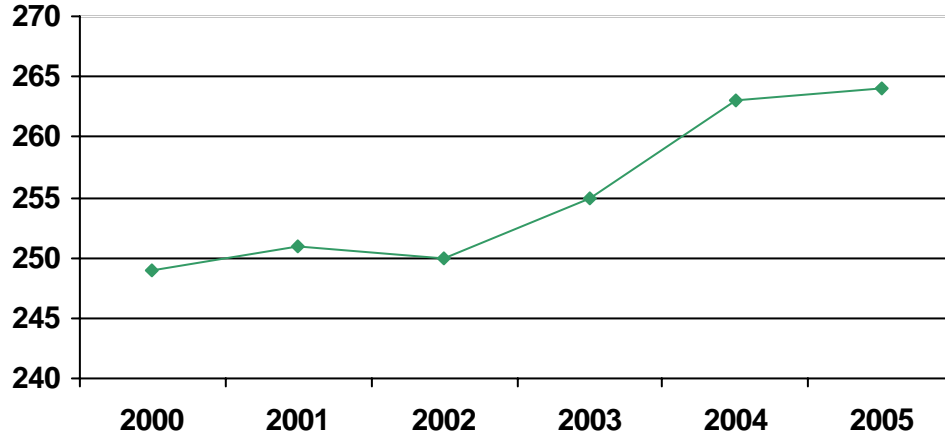
Figure 4. Number of active RCW clusters in the western subpopulation, 2000-2005.

The estimated number of groups in the population is a less reliable indicator of population size than number of active clusters because whether an active cluster contains a group is known only for recruitment clusters and the donor plots. Outside of the donor plots, the proportion of active clusters (excluding recruitment clusters) that contain groups, as opposed to containing unpaired males or being captured, must be estimated from the monitoring sample. The estimated number of groups increased more proportionally over the five years of the study than did the number of active clusters (8.5% compared to 6.7%), but followed a much more erratic trajectory (Figure 5). Surely the more erratic trend of this estimator is due to a large extent to sampling error rather than real differences between years in the proportions of active clusters occupied by groups. We conclude that population increases indicated by number of active clusters and estimated number of groups are comparable, and that the former is the more accurate indicator of population behavior.
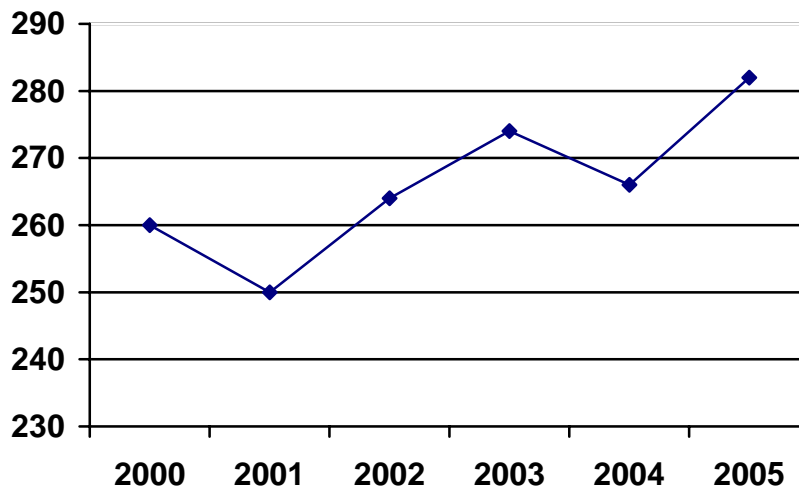
Figure 5. Estimated number of RCW potential breeding groups, 2001-2005.

A closer examination of changes in cluster status reveals that recruitment cluster construction did fuel population gains (Figure 6), but the gains that were achieved were compromised by higher than expected rates of cluster abandonment. The natural processes of new territory formation of budding and pioneering resulted in the addition of only eight active clusters over the course of the study, which translates into a population growth rate of 0.05% per year. Low rates of pioneering and budding were expected based on our previous management experiment, as rates below 1% per year were observed in plots in which recruitment clusters were available, as they were in all portions of the base during this study.

Recruitment cluster construction added 48 active clusters to the population over the course of the study. Population growth through this activity was 3.9% per year in the eastern subpopulation, and 2.8% per year in the western subpopulation. Although the rate of population growth through recruitment cluster construction is far below the target (10%) in the eastern subpopulation, it is close to the target (4%) in the western subpopulation. The rates would have been closer to the targets except that abandonment of recruitment clusters exceeded reoccupation (Figure 6). In our previous study these processes were balanced, reflecting the dynamic nature of the initial occupation of recruitment clusters (Walters et al. 2004), whereas in the current study these processes resulted in a net loss of 11 clusters, counterbalancing a significant fraction of the 59 instances of initial recruitment cluster occupation (Figure 6).

Of more significance than this was the imbalance between abandonment and reoccupation of previously existing clusters, which resulted in a net loss of 35 clusters over the course of the study (Figure 6). We anticipated that cavity management would prevent permanent territory abandonment, and that temporary abandonment would be balanced with reoccupation. Instead, in both the eastern and western subpopulation, losses through an imbalance between abandonment and reoccupation exceeded those observed in any of the treatments in the previous study (Table 1). In the previous study, losses to territory abandonment were observed in only two treatments (Table 1), and one of those treatments (western high intensity) did not include cavity management. In two

other treatments, reoccupation exceeded abandonment, so that these processes resulted in net gains rather than losses (Table 1). Only in the low intensity treatment in the eastern subpopulation were high rates of loss to abandonment observed despite cavity management. We attributed that result to a shortage of birds to replace breeders that died due to the fact that many potential replacement breeders were instead occupying the many recruitment clusters located in these plots, and no birds were translocated to these plots to supplement the pool of potential replacement breeders (Walters et al. 2002a). A similar explanation does not suffice for the western subpopulation in the current study because the number of recruitment clusters relative to existing population size was not large enough to impact the pool of potential replacement breeders sufficiently. It does not suffice for the eastern subpopulation because translocation was employed there.
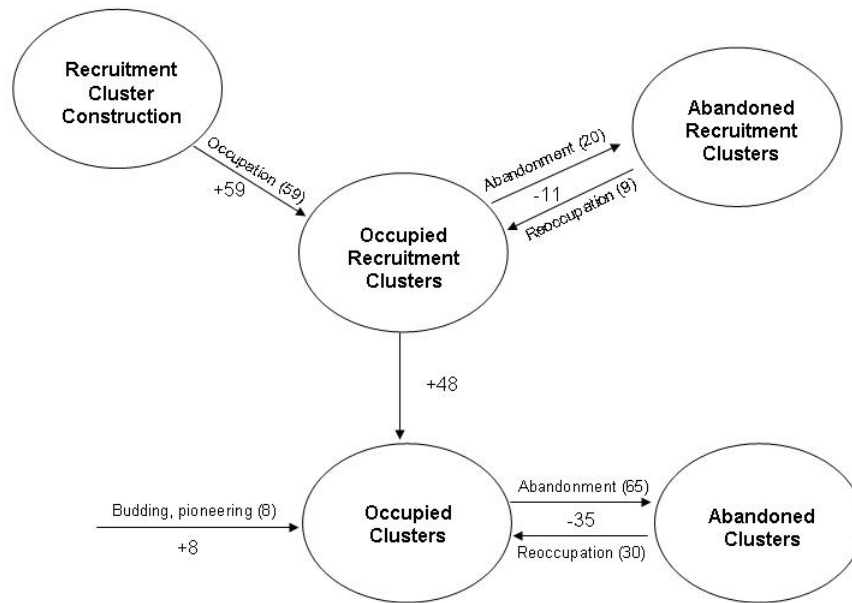
Figure 6. Changes in numbers of active clusters between 2000 and 2005. Numbers in parentheses are the number of events of the type indicated, and numbers accompanying arrows indicate the net change in cluster number resulting from the indicated transition.

We therefore conclude that there were significant differences in population dynamics between the five years of the study and the preceding five years, which resulted in more losses to territory abandonment and fewer gains from recruitment cluster construction during the current study. We will return to this theme in the Conclusions section below, after examining other data that bear on the mechanisms that may be behind the change in population dynamics.

Table 1. Proportional changes in number of active clusters due to the processes of cluster abandonment and reoccupation, new cluster formation through budding and pioneering, occupation of recruitment clusters, and the sum of these processes (Total Growth), for the eastern (East Current) and western (West Current) subpopulations during the current study (2000-2005), and for the five experimental treatments (East Low = lower intensity management in eastern subpopulation; East High = higher intensity management in eastern subpopulation; West Low = lower intensity management in western subpopulation; West High = higher intensity management in western subpopulation; Donor = donor plot; see Walters et al. 2002a) in our previous study (1995-2000).

Treatment	Reoccupation - Abandonment	Budding + Pioneering	Recruitment Clusters	Total Growth
East Low	- 10%	+ 3%	+ 60%	+ 53%
East High	0	+ 4%	+ 69%	+ 73%
West Low	+ 1%	+ 9%	0	+ 11%
West High	- 10%	+ 7%	+ 35%	+ 32%
Donor	+ 8%	+ 4%	0	+ 12%
East Current	- 12%	0	+ 21%	+ 10%
West Current	- 12%	+ 3%	+ 15%	+ 6%

Population Structure and Demography

   Population structure and demography affect the capacity of populations to respond to management. Specifically in the case of the RCW, capacity for population growth is dependent on the number of non-breeding adults (i.e., helpers and floaters) and fledglings available to occupy recruitment clusters. Three useful indicators of this capacity are (1) group size, which is a direct measure of the number of helpers in the population; (2) productivity, which is a direct measure of the number of fledglings in the population; and (3) retention of breeding males, which is a direct measure of the number of other (i.e., besides unoccupied recruitment clusters) breeding vacancies available to males. When more such vacancies are available, capacity to occupy recruitment clusters is reduced. Also, rate of retention of breeding males can be viewed as a survival estimate, because breeding males almost never disperse (Walters 1990). Annual variation in survival is not highly correlated among different status classes in RCWs (e.g., Walters et al. 2005), so breeding male survival is not a reliable indicator of the survival of the helpers, floaters and fledglings that occupy recruitment clusters. It is nevertheless useful as a general indicator of changes in demography over time, in this case between our previous study (1995-2000) and the current study (2000-2005).

   Data on group size, productivity and retention of breeding males come from breeding season monitoring. There are thus three potential sources of such data, recruitment clusters, the donor plots and the monitoring sample. We do not use data from recruitment clusters because typically they are occupied by young birds, resulting in low productivity and small group sizes initially (Walters et al. 1995; 2004). Thus their demography is characteristic of recruitment clusters rather than representative of the population. The monitoring sample is designed to produce population-wide estimates of group size, but because adults are counted but not banded and nesting is not monitored, it provides no data on productivity or retention of breeding males. The donor plots provide the only estimates of theses two parameters, as well as an additional estimate of group size. We

recognize however that estimates from the donor plots may not be representative of the entire population, because on the donor plots group sizes are reduced by removal of juveniles that could potentially become helpers for translocation, and group size affects productivity (Walters 1990) and breeder survival (Khan and Walters 2002). Nevertheless estimates from the donor plots are useful as indicators of trends over time.

Because recruitment clusters induce helpers seeking breeding opportunities to disperse from their natal groups, their presence tends to reduce average group size. During our previous study, in plots without recruitment clusters group sizes increased dramatically, a trend we attributed to improvements in habitat quality achieved by prescribed burning and other elements of ecosystem management (Walters et al. 2002a). In plots with recruitment clusters, group sizes increased only in those plots in which translocation was employed. In plots with recruitment clusters but no translocation, group sizes were best characterized as stable (Walters et al. 2002a). Based on these results and the management strategies applied to the two subpopulations during the current study, we expected group sizes to increase in the eastern subpopulation and to remain stable in the western subpopulation. This should have translated into slightly increasing group sizes in the monitoring sample, and stable group sizes on the donor plots. Instead, group sizes in the monitoring sample remained stable and group sizes in the donor plots declined (Figure 7). The apparent recovery in group size on the donor plots in 2004 is deceiving: this is due entirely to the addition of plot 8, where average group size was 3.52, to the donor plots. Average group size on the other two donor plots in 2004 was 2.43, the same as it had been in 2003 (Figure 7). We conclude that population performance with respect to this parameter was below expectation.
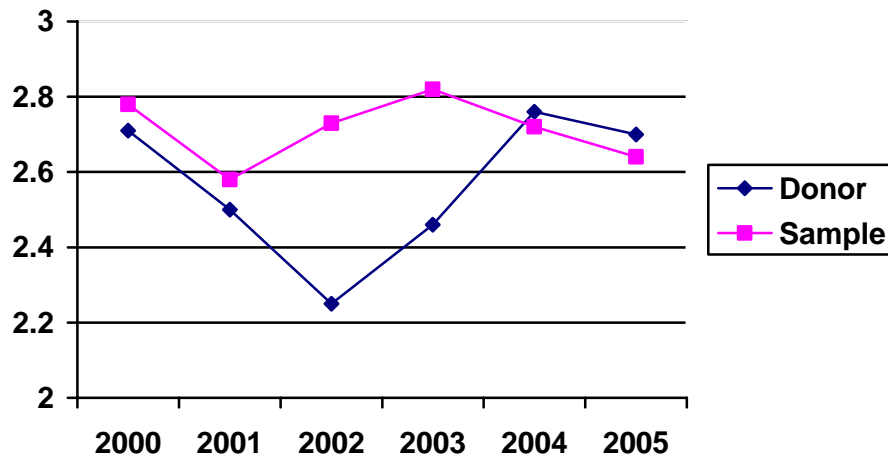
Figure 7. Average group size on the donor plots (Donor) and in the monitoring sample (Sample) from 2000 through 2005. Solitary males are included as groups of one.

Productivity on the donor plots generally was below average during the study. Whereas in the previous five years productivity was above 1.4 fledglings per potential breeding group each year except the drought year of 2000, it was below this value in three of the five years of the study, and was well above it only in the last year (Table 2). The fledglings from this last year of course were not available to occupy recruitment clusters during this study, but will be beginning in 2006. The poor productivity of 2000,

on the other hand, did impact occupation of recruitment clusters during this study. Not only did it result in low availability of fledglings to occupy recruitment clusters in 2001, but we believe it also is responsible for reduced group sizes in 2001 compared to 2000 (Figure 7), which resulted in a continuing, albeit diminishing, reduction in capacity for recruitment cluster occupation in subsequent years. However, group size does not track productivity after 2000-2001, and group sizes had rebounded by 2003. Although relatively few fledglings were available to occupy recruitment clusters in four of the five years of the study, we conclude that relatively poor productivity cannot account for continued low rates of population growth beyond the first few years.

Table 2. Number of fledglings produced per potential breeding group (Groups) on the donor plots, 2000-2005. Groups occupying recruitment clusters within the donor plots are not included in these data.

Year	2000	2001	2002	2003	2004	2005
Groups	27	41	43	41	64	52
Fledglings/Group	1.19	1.44	1.23	1.32	1.30	1.54

During the previous study, the annual rate of retention of breeding males, both population-wide and for the donor plot specifically, was 76% (Walters et al. 2002a). The rate of retention of breeding males on the donor plots during the current study varied somewhat among years, but was nearly identical overall, averaging 77% (Figure 8). We conclude that there was no significant change in rate of retention of breeding males between the five years of this study and the previous five years, and thus that reduced population growth was not due to greater availability of breeding vacancies for males.
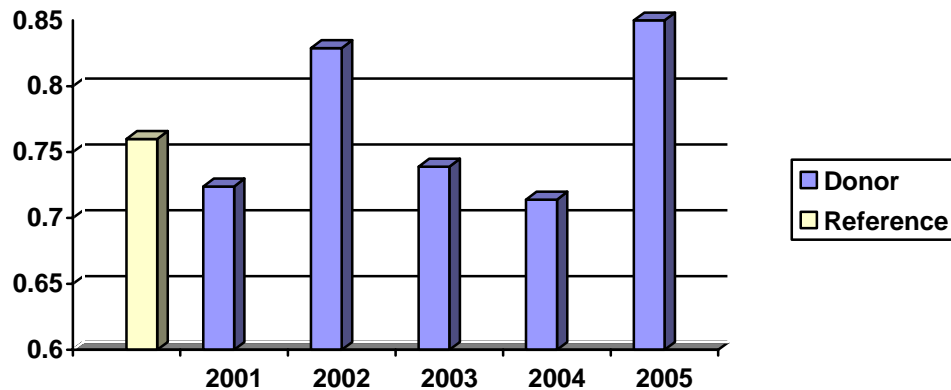
Figure 8. Annual probability of retention of breeding males on the donor plots (Donor) from 2001 through 2005. Values are the probability that the breeding male present in the year indicated is the same male as in the preceding year. The average value for the preceding five years (1995-2000) is indicated for comparison (Reference).

Overall the data suggest demographic conditions for population growth were relatively poor during the early years of the study, but had improved by the end. The differences between the study period and the preceding five years when population growth was rapid are not great, however, suggesting that relatively poor demographic

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conditions may have contributed to the observed reduction in population growth rates, especially early on, but are not sufficient to explain it. We conclude that other factors must have been the fundamental causes of poor population growth.

Response to Management Techniques

The basic techniques used to monitor the number of active clusters in the population, which include cluster activity checks, inactive cluster surveys, budding checks and pioneering surveys, have now been employed for many years on Eglin. During the current study these techniques resulted in the regular discovery of new clusters formed by budding and pioneering, and changes in cluster activity status from inactive to active. We believe these techniques are highly effective, and therefore that annual values for population size as measured by number of active clusters are extremely accurate. Thus we conclude that the low population growth rates over the past five years represent a true change in population behavior rather than a reflection of sampling error.

In order to further investigate the causes of reduced response to management, we evaluated the effectiveness of the key management techniques employed on Eglin.

Recruitment Clusters. – Occupancy of recruitment clusters is the key to population increase, and we established standards for the effectiveness of recruitment clusters in the previous study based on improvements in locating and constructing recruitment clusters and observed response to them. Our performance objectives were a 75% probability of occupancy of recruitment clusters within three years of construction, and an annual occupancy rate of 30% of available recruitment clusters (Walters et al. 2004).

Recruitment clusters were fairly equitably distributed across the population in the current study, whereas in the previous study they were concentrated in certain plots. The amount of recruitment cluster construction during the study was similar to that in the previous study, however. In the previous study 10-15 recruitment clusters were constructed per year, compared to 8-17 during the current study. The response to recruitment clusters also was similar, and occupation targets were achieved. Combining all years, 71% of newly constructed recruitment clusters were occupied within three years, and the annual probability of occupancy was 39%. Although there was some variation from year to year, occupancy was never far below the targets in any year, and exceeded the targets in several years (Figure 9). Clearly poor population growth was not due to a failure to attract birds to new recruitment clusters.

Although recruitment clusters were as effective at attracting birds as previously, they were not as effective at retaining these birds. As shown above, the processes of abandonment and reoccupation of recruitment clusters resulted in a net loss of active clusters (Figure 6). During the previous study, occupation of recruitment clusters was somewhat dynamic initially, with 12% being abandoned after one year of occupation, but if birds remained in them a second year they were likely to remain occupied. The probability of abandonment after two years of occupancy was only 2%, and it was only 3% after three years of occupancy (Walters et al. 2004). During the current study probability of abandonment after one year was similar (10%, n = 50), but it jumped to 12% after two years of occupancy (n = 51) and 6% after three years of occupancy (n = 48). Thus, just as with normal clusters (see above), among recruitment clusters an increase in rate of abandonment between the current study and the previous one is

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evident. Increased cluster abandonment clearly was a major contributor to reduced population growth over the last five years.
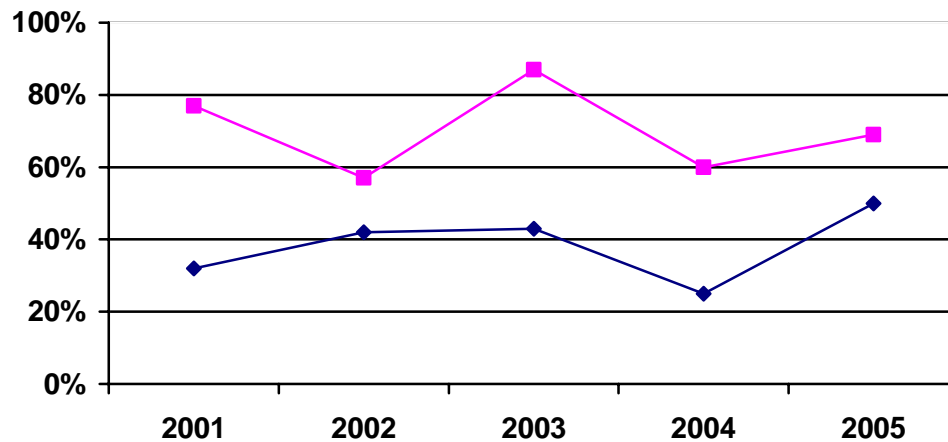
Figure 9. Rates of occupation of recruitment clusters. The upper line shows the proportion of recruitment clusters constructed three years previously that had been occupied by the year indicated, and the lower line shows the proportion of previously unoccupied recruitment clusters occupied in the year indicated. The objective for the former was 75%, and for the latter 30%.

Translocation. – During the previous study each winter we were able to locate 5-8 juveniles eligible to be translocated on a single donor plot (9). We obtained one juvenile per 2.6-4.4 (mean = 3.8) potential breeding groups, and 14-35% (mean = 21%) of the fledglings produced on the donor plot were eligible for translocation (Table 3). This number of translocated birds proved sufficient to produce a positive impact on population growth in the three plots to which birds were moved (Walters et al. 2002a). We translocated birds in fall as well as winter for the first time in the nonbreeding season (2000-2001) spanning the transition between our previous study and the current one. We were only able to locate four birds eligible for translocation that winter, which represented 12% of the fledglings produced on the donor plot, or one eligible bird per 6.8 potential breeding groups (Table 3). The birds captured in fall were translocated to other populations as part of a regional translocation strategy, in which Eglin participated for the first time as a donor population. Six birds were donated to the program in 2000-2001, so overall 10 birds were translocated that year, representing 31% of the fledglings produced on the plot, or one bird per 2.7 potential breeding groups (Table 3). It thus seemed initially that adding fall translocation increased the number of birds moved, but decreased availability of birds in winter.

Adoption of the basewide management strategy increased the number of recipient plots for translocation within Eglin from three to four. Both this change and donating birds to the regional translocation effort increased the demand for birds for translocation. Furthermore, it appeared likely that donating birds for regional translocation in fall would reduce ability to meet the needs of Eglin's within population translocation effort in

winter. To address these changing demands, a second donor plot (7) was established, and it began contributing birds for translocation in 2001-2002.

Table 3. Numbers of birds translocated from donor plots in fall, winter and the whole non-breeding season (Total) for each year indicated. For Winter and Total, the number of monitored groups per bird moved (Groups/Bird), and the proportion of the juveniles produced on the plots moved (% Juveniles), are also indicated. The five years of the previous study are combined (1995-2000) and ranges over the five years are shown.

	1995-2000	2000-2001	2001-2002	2002-2003	2003-2004	2004-2005
Fall						
Number	0	6	4	2	2	3
Winter						
Number	5-8	4	7	1	3	0
Groups/Bird	2.6-4.4	6.8	5.9	43.0	13.7	-
% Juveniles	14-35%	12%	12%	2%	6%	0%
Total						
Number	5-8	10	11	3	5	3
Groups/Bird	2.6-4.4	2.7	3.7	14.3	8.2	13.3
% Juveniles	14-35%	31%	19%	6%	9%	6%

We anticipated that with the addition of a second donor plot there would be 10-12 birds available each year, half of which would be used for within population translocation in winter. Unfortunately, this did not prove to be the case. In the first year that two donor plots were used (2001-2002 non-breeding season) the expected number of birds was indeed available for within population translocation in winter, despite donating four birds to regional translocation in the fall (Table 3), and thus the new translocation strategy appeared to be working well. However the next two years almost no birds eligible for translocation could be located in winter, even though only two birds were donated to the regional translocation effort each year. The number of groups monitored per bird obtained for translocation jumped well above previous values, and the proportion of juveniles on the plots used dipped well below previous values (Table 3).

To attempt to address this breakdown of the translocation effort, the third donor plot (8) was established in 2004, and a new translocation strategy was adopted. Each year one of the three plots would serve as the source of birds for fall translocation, the second would serve as the source of birds for winter translocation, and the third would not be used. The plots would rotate through these three functions from year to year. This new strategy was employed in the last year of the study (2004-2005 non-breeding season) but without success, as it produced no more juveniles for translocation than there were the previous two years (Table 3). We conclude that an inability to locate sufficient juveniles eligible for translocation in order to execute the management strategy in the eastern subpopulation contributed to failure to achieve desired population growth rates there. Note that growth of the eastern subpopulation was reasonable during the first two years of the study, but ceased once the translocation program failed (Figure 3). The deficiencies in the translocation program cannot account for poor growth of the western subpopulation, however, so clearly it is not the only contributing factor.

In addition to being reduced in scope due to an inability to locate birds eligible to be moved, the effectiveness of translocation also may have been reduced compared to the previous study. In the previous study, 77% of 31 translocated birds were known to be alive the subsequent breeding season, 19% were still in the cluster to which they were moved, and an additional 39% were still in the plot to which they were moved (Walters et al. 2004). Only 50% of the birds moved during 2000-2005 (n = 18) were known to be alive the next breeding season, 22% in the cluster to which they were moved and an additional 17% within the plot to which they were moved. One possibility is that birds that left the translocation site had a greater difficulty locating another group to join than in previous years, and therefore suffered greater mortality. It is also possible the difference is accounted for by birds that remained alive but were not detected, since the proportion of clusters monitored in the recipient plots was less than in the previous study. We conclude that reduced translocation success may have been a minor factor contributing to reduced population growth rates in the eastern subpopulation compared to our previous study, but was not nearly as important as reduced translocation effort.

What might account for the paucity of birds obtained for translocation? Poor survival of juveniles could produce such an effect. Because many groups on Eglin are not censused, it is difficult to distinguish mortality from dispersal and thus estimate survival rates accurately. This is especially problematic for juvenile females since nearly all of them disperse from their natal groups in their first year, and therefore we will not attempt to assess juvenile female survival. For juvenile males, however, the proportion of birds retained in their natal groups as helpers can be used as an indicator of survival, since birds retained as helpers account for the majority (e.g., 64% in the North Carolina Sandhills, Walters 1990) of juvenile males that survive to age one. Because some juvenile males are removed from their groups for translocation, one expects the proportion of males retained as helpers to be reduced in the donor plots, but the sum of males retained and males removed ought to equal or slightly exceed the proportion of males retained in normal circumstances. Indeed, in the first two years of the study when we were able to locate birds for translocation, the sum of males removed and males retained on the donor plots exceeded (2000-2001) or was comparable to (2001-2002) the value for males retained obtained from the monitoring sample during our previous study (Table 4). However in the remaining three years when availability of birds for translocation was poor (2003-2004; 2004-2005), the proportion of males moved was much less and the proportion retained as helpers no higher, so that the sum of the two was well below the normal retention rate (Table 4). Evidently it was not the case that we simply failed to locate birds that could have been moved, as this would have been reflected in a higher proportion of birds remaining in their natal clusters. Instead, it appears that in those years when we were unable to locate juveniles for translocation, either juvenile male mortality rates were higher or more juvenile males were dispersing from their natal clusters than previously.

To further investigate population dynamics on the donor plots, we examined helper male retention rates, that is, the proportion of helper males that remained in their groups from one year to the next. Similar to juvenile males, some helper males disperse each year, but the majority of helpers that survive from one year to the next remain in the same group (e.g., 82% in the North Carolina Sandhills, Walters 1990), most remaining in helper status and some inheriting breeding status. A pattern similar to that for juvenile

males is evident in these data: helper male retention rate on the donor plot was high in the first year of the study, but was much lower than is typical for the species thereafter, except for the last year of the study (Table 5).

Table 4. The proportion of juvenile males retained as helpers in their natal groups at age one (Retained), the proportion translocated to other clusters (Translocated) and the sum of these two values (Total), for each year and the average among years (Mean) on the donor plots, for the monitoring sample during 1995-2000 (Eglin), and for two reference populations in North Carolina, Camp Lejeune (CL) and the Sandhills (SH). Data for the reference populations are from Walters (unpublished).

	Donor								
	00-01	01-02	02-03	03-04	04-05	Mean	Eglin	CL	SH
Retained	31%	26%	28%	30%	23%	28%	47%	45%	34%
Translocated	23%	16%	6%	7%	2%	11%	0%	0%	0%
Total	54%	42%	34%	37%	26%	39%	47%	45%	34%

Table 5. The proportion of helper males retained in the same group from one year to the next, for each year and the average among years (Mean) on the donor plots, for the monitoring sample during 1995-2000 (Eglin), and for two reference populations in North Carolina, Camp Lejeune (CL) and the Sandhills (SH). Data for the reference populations are from Walters (unpublished).

Donor								
00-01	01-02	02-03	03-04	04-05	Mean	Eglin	CL	SH
75%	41%	47%	44%	57%	53%	61%	62%	62%

The helper male retention data suggest the same possibilities as the juvenile male data: either mortality was higher than normal on the donor plots during much of the study, or more birds than usual dispersed from their groups. If mortality was elevated, it was elevated only for juveniles and helpers, but not breeding males, as breeding male retention rates, which are virtually identical to survival rates, were normal. We know of no mortality factor likely to impact juvenile and helper males more than breeding males. Thus elevated dispersal seems a more likely possibility, and there is one obvious factor that could increase dispersal of both juvenile males and helper males without impacting breeding males, the presence of recruitment clusters. In the previous study recruitment clusters were not constructed in the donor plot, whereas 12 recruitment clusters constructed in the three donor plots were occupied during the current study, drawing birds that might otherwise have been available for translocation (i.e., juveniles of both sexes, helper males and floater females) away from their groups.

We anticipated based on our previous study that on the donor plots the combination of removing birds for translocation and occupying recruitment clusters would prevent any increase in group size, but that both population growth and level of translocation effort could still be sustained. But under the poorer level of base-wide population performance that characterized the current study, both occupation of recruitment clusters and production of birds for translocation could not be supported simultaneously. Group sizes declined under these dual pressures, eliminating the pool of "excess" birds that could be used for translocation. Furthermore, as group sizes decline and fewer groups contain

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non-breeding members, the chances that a deceased breeder must be replaced by a bird dispersing from elsewhere rather than from within the group increases, further elevating dispersal rates. This, as well as the presence of recruitment clusters, likely contributed to reduced retention of juvenile males and helper males on the donor plots (Table 4 and 5). The end result is that the remaining non-breeders are spread more evenly among the groups on the donor plots, so that fewer of them qualify as "excess". Allowing donor plots to "recover" by not using them in one year out of three may help alleviate this problem by enabling at least some groups to increase to larger sizes, but it may be necessary to refrain from constructing recruitment clusters in donor plots as well, so that they can retain their function as a source of birds for translocation to support population growth in the eastern subpopulation. Note that this explanation of the deficiencies in the translocation program leaves unanswered the cause of the reduction in population performance base-wide. It is a contributing factor to the poor performance of the eastern subpopulation, but is not sufficient to account for it, and is irrelevant to the poor performance of the western subpopulation.

Ecosystem Management. – Our research did not include assessment of improvements in habitat condition achieved through Eglin's ecosystem management program, so we cannot analyze quantitatively its contribution to population behavior. Qualitatively it is obvious that the enormous amount of prescribed burning specifically and forest management generally have changed the character of longleaf habitat considerably during the study. Especially significant are reduced hardwood midstory and a richer and more diverse groundcover on thousands of acres, and reduction in sand pine in some areas. These changes have increased the amount of nesting habitat available to support population growth. They also have improved foraging habitat quality on many RCW territories, which based on previous research is expected to increase productivity and group size (Hardesty et al. 1997; James et al. 1997; 2001; Walters et al. 2002c; Convery 2002). We proposed in our previous study that similar improvements in habitat quality were indeed resulting in increased group sizes on Eglin, which was particularly evident in plots that lacked recruitment clusters (Walters et al. 2002a). The lack of continued increases in group size despite further improvement in habitat quality is another indicator of the drop in population performance during the current study.

Ecosystem management, specifically prescribed burning during the growing season, had one unintentional, potentially negative impact on RCWs. The return of growing season fire to an ecosystem in which it has been long suppressed is problematic, due to the excessive fuels that build up in the absence of fire. Although Eglin's growing season burning program has been highly successful in terms of reducing hardwood midstory and promoting groundcover development in areas that had not been burned for decades, it has occasionally resulted in fires that were hot enough to kill mature pines, including the old growth pines upon which RCWs depend for cavity excavation. The frequency of such events has declined over time as fuels have been reduced by repeated burning and burning techniques have become more sophisticated, but losses of cavity trees and other old growth pines to fire did occur during the study. This relates directly to the final management technique we will discuss, cavity management.

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Cavity Management. – The most striking characteristic of the cavity management program is the amount of effort required. Based on application of cavity management to six plots in our previous study, we anticipated that considerable effort would be needed initially to bring clusters in the nine previously untreated plots up to the required number of good cavities, but that after this initial effort the number of clusters requiring treatment annually would be fairly low. The annual effort required stabilized at 8% of active clusters in the last years of the previous study (Walters et al. 2002a). Initially this prediction appeared accurate. Annual effort increased between the first year and the second as a result of increasing the required number of good cavities from three to four, but fell to the anticipated level of 8% by the third year (Table 6). However, the next year many cavities were lost to two hurricanes, greatly increasing the amount of cavity management required. In fact, the demand for cavity management was so great in 2004 that we were unable to provide additional cavities in all of the clusters that required them. By allocating greater effort to cavity management in 2005 we were able to "catch up" with losses to hurricanes the previous year, as well as subsequent losses. The end result was that > 10% of the clusters required treatment in four of the five years of the study, and nearly 20% required treatment in two of the five years (Table 6).

Table 6. Clusters requiring cavity management each year, expressed in terms of both the number and proportion of active clusters requiring treatment. The total number of cavities added through drilling new cavities or restricting enlarged cavities is also indicated. Year indicates the breeding season in which the deficiencies treated were identified. Treatment was applied between that breeding season and the next.

Year	Proportion of Active Clusters Treated	Number of Clusters Treated	Number of Cavities Drilled or Restricted
2001	12%	38	54
2002	18%	55	100
2003	8%	26	52
2004	13%	41	78
2005	19%	60	92

These results are significant because we have identified cluster abandonment, which cavity management is designed to prevent, as a critical factor contributing to low population growth rates during the study. There is a lag time between the point at which clusters become deficient in cavity number and the point at which the deficiency is corrected through cavity management. First, deficiencies are identified during tree checks at the beginning of the breeding season, but the cavity losses that resulted in these deficiencies could have occurred at any time within the year since the previous tree checks. Second, cavities cannot be replaced until winter when reduced resin flow enables cavity drilling, so replacement does not occur until 7-9 months after deficiencies are identified. Hence, some clusters may be deficient in cavity number for over a year before the problem is corrected through cavity management.
     Instances of cavity deficiency may have three different outcomes. First, in many cases the birds correct the deficiency themselves by excavating new cavities, so that territory abandonment does not occur. Indeed, each year the number of clusters identified as requiring treatment substantially exceeds the number actually treated, due to

the birds' excavation of new cavities between the time of tree checks and the cavity drilling season. Second, the deficiency may not be severe enough to cause the birds to abandon the cluster right away, in which case cavity management will be effective in correcting the problem. This is the situation for which cavity management is best suited. Third, the deficiency may be so severe (e.g., 0-1 good cavities remain) that the birds abandon the cluster quickly, before treatment can be applied, so that continued use becomes dependent on the reoccupation process. It is cases of this third kind that are problematic, and they are a minority. As long as the number of clusters requiring treatment is kept low, i.e. under 10%, the minority of cases that result in abandonment will not impact population growth much. But during this study the proportion of clusters requiring treatment exceeded 10% in four of the five years, indicating that cavity losses were exceeding the capacity of cavity management to address them much of the time.

The answer to this dilemma is to reduce cavity losses to a manageable level. Hurricanes are an important source of loss that can create severe deficiencies in affected clusters, and they cannot be managed. However, because of their seasonality, losses to hurricanes can be compensated through cavity management relatively quickly, only 1-6 months after the loss occurs, if losses are identified immediately after the storm and deficiencies corrected as soon as possible thereafter. Eglin now has a policy in place to do just that: not only will lost cavities be identified immediately and replaced the next drilling season, but if loss is severe in some clusters insert boxes (Allen 1991), which do not have the seasonal constraints that drilled cavities do, will be provided immediately to those clusters. Normally drilled cavities are preferred over insert boxes because of their greater durability (USFWS 2003; Hooper et al. 2004), but in this case their use is well justified because of immediate need. We believe that this policy will prevent cavity losses to hurricanes from causing territory abandonment.

Excepting hurricanes, cavities are otherwise lost to either cavity tree mortality or enlargement by other species. In two North Carolina populations, losses to cavity tree mortality were about 5% annually, whereas losses to cavity enlargement were roughly equal to losses to cavity tree mortality in one case and twice as high in the other (Walters and Harding 2002). On Eglin losses to tree mortality appear to dominate, and mortality rates appear to be greater than in the North Carolina populations. It may be that during the five years of the study cavity tree mortality rates were high enough that cavity management was not sufficient to adequately address them, resulting in unacceptable levels of territory abandonment. Some losses of cavity trees, such as those to lightening strikes, are inevitable, but can be effectively compensated through cavity management because they are isolated and relatively few in number. Losses to fire are more problematic because they can be patchy, resulting in severe cavity deficiencies in affected clusters, and can occur in larger numbers. Eglin now has a policy in place to immediately replace cavities destroyed in a fire with insert boxes, as with hurricane losses. However, such immediate losses are rare. More problematic is delayed mortality resulting from stresses imposed on cavity trees by exposure to hot fires. We believe that such cavity tree mortality resulting from fire contributed to the unexpectedly high rates of territory abandonment that occurred during the study.

To reduce territory abandonment in the future, we recommend continuing the current policy for response to direct losses to hurricanes and fire, making every effort to reduce delayed cavity tree mortality resulting from prescribed burning to a minimum, and

improving cavity management procedures. There will probably always be some losses to wildfire, but improved burning techniques and effective protection of cavity trees during burns can reduce or even eliminate prescribed fire as a source of mortality. Cavity management procedures can be improved by inspecting inactive cavities counted as suitable. We counted all unenlarged inactive cavities that appeared intact from exterior inspection as suitable. If some such cavities are in fact unsuitable due to deterioration or damage to the cavity interior, cavity deficiencies will be underestimated, increasing the risk of territory abandonment. Eglin has now eliminated this problem by altering the cavity management procedure to include interior inspection of inactive cavities that could potentially be considered suitable.

Conclusions

The objectives of applying the base-wide management strategy for RCWs on Eglin and measuring population growth rate in response to it were achieved, but the growth rates produced were below targets in both the eastern and western subpopulations. Lower than expected population growth was not due to any reduction in effectiveness of recruitment clusters, but rather to unexpectedly high rates of territory abandonment and reduced effectiveness of translocation.

Translocation was less effective than previously due mostly to reduced effort, that is, inability to locate birds to move, rather than to reduced success in moving birds to desired locations. To correct this deficiency we recommend refraining from constructing recruitment clusters in donor plots, in order to avoid drawing that birds that might otherwise be moved away from their natal groups. We also recommend sustaining three donor plots, and using only two of them in any given year, to increase mean and variance in group size, which will increase the number of birds eligible for translocation.

High rates of territory abandonment indicate that cavity management was not completely effective. To address this problem we recommend attempting to eliminate cavity tree mortality resulting from prescribed burning, and continued emergency cavity management in response to hurricane damage. The existing cavity management program should be sufficient to compensate for other causes of cavity loss and thereby prevent territory abandonment. Relatively poor productivity may have been a contributing factor to high rates of territory abandonment, but not a root cause. Relatively poor survival may have contributed similarly, but evidence for reduced survival is equivocal.

Although population performance was disappointing relative to the previous five-year period, population size nevertheless increased during the study, and its distribution improved in that new territories added to the population increased the spatial aggregation of territories in the eastern subpopulation (Figure 10). Spatial aggregation of territories has a strong positive impact on the stability of small RCW populations (Letcher et al. 1998; Walters et al. 2002b), and increasing the stability of the eastern subpopulation is one of Eglin's primary RCW management objectives. On the other hand, the connection of the eastern subpopulation to the larger western subpopulation was not strengthened during the study during the study and possibly weakened due to abandonment of several territories in the center of the base on plots 2 and 3 (Figure 10). Improving the connection between the two subpopulations also is a primary management objective. Because of lack of progress toward this objective, it remains necessary to continue to manage the eastern subpopulation as a self-sustaining unit.
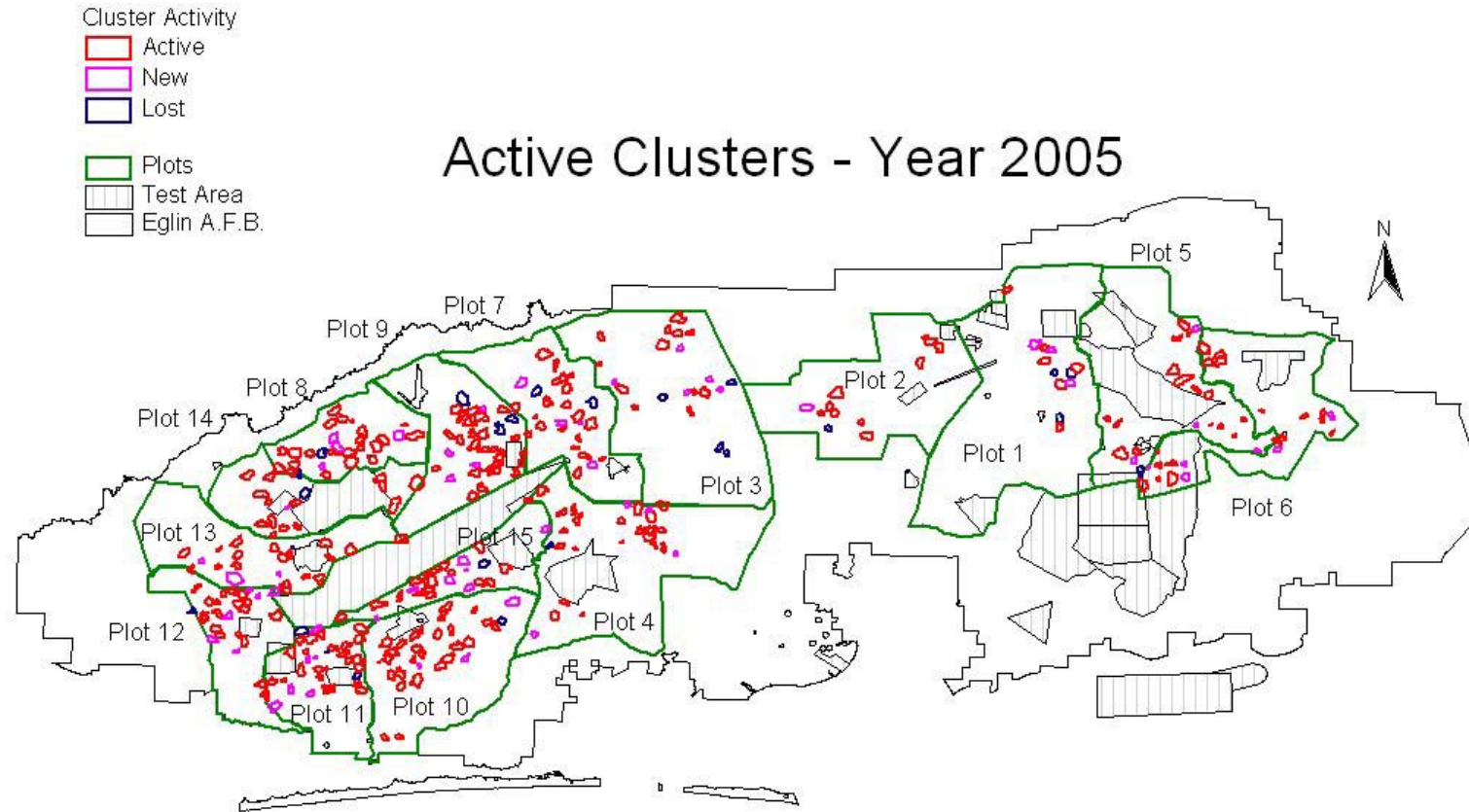
Figure 10. Active red-cockaded woodpecker clusters on Eglin Air Force Base in 2005. New clusters that were established (New) and previously existing clusters that were abandoned (i.e., inactive for ≥ 3 years) during the study (Lost) are shown. Study plots are indicated by number, and military test ranges that contain some cleared areas are shown (Test Area).

Despite some disappointing results in recent years, Eglin's red-cockaded woodpecker population remains headed toward recovery, and it is closer to recovery now than it was at the outset of the study. We believe that with the slight adjustments in management strategy suggested by our analyses (i.e., increase translocation effort, reduce cavity tree mortality) higher rates of population growth can be achieved and progress toward recovery can be accelerated.

EXPERIMENTAL STUDY OF THE CAVITY-NESTING COMMUNITY
Background

Cavity-nesting species comprise a major component of the bird community at Eglin. Being both stewards of the ecosystem and responsible for recovery of the endangered red-cockaded woodpecker, Eglin managers must be concerned about possible conflicts between ecosystem management and single-species management. It is clear that prescribed growing season fire benefits not only RCWs, but also most other species inhabiting longleaf forests (Provencher et al. 2001; Conner et al. 2001; Allen et al. 2006). In contrast, how cavity management and recruitment cluster construction affect other species is unknown. There is potential for positive benefits to other cavity users, but on the other hand restricting cavities so that larger species cannot use them may have negative effects on some species. In some locations, although not at Eglin, other cavity users are persecuted because of perceived negative effects on RCWs (Franzreb 1997). In fact, the nature of the relationships of RCWs with other cavity users is poorly known (USFWS 2003).

Cavity-nesting communities contain several guilds. Primary cavity excavators (PCEs) such as RCWs excavate their own cavities, whereas secondary cavity nesters (SCNs) such as American kestrels (*Falco sparverius*) rely on cavities excavated by other species or natural holes. Weak cavity excavators (WCEs) such as brown-headed nuthatches (*Sitta pusilla*) use cavities produced by PCEs, but also excavate some of their own cavities. Thus cavity nesters exhibit a clear hierarchy with potentially strong interdependencies among species. Some species depend partly (WCEs) or wholly (SCNs) on others for a critical resource, nesting sites. Cavity-nesting communities seem well suited to community analysis, but they have not been well studied from this perspective. Studies of differences among species in resource use and resource overlap exist (e.g., Van Balen et al. 1982; Angelstam 1990; Dobkin et al. 1995; Sedgwick 1997), but these studies are descriptive. Few have directly examined the links among species or the mechanisms that structure these communities.

Following Martin and Eadie (1999) in this study we apply methods traditionally used to study food webs to the "nest webs" of the cavity-nesting community. Food webs are characterized by a central resource, a hierarchy of consumers of that resource, and links between species within and between levels of the hierarchy (i.e., trophic levels). For the cavity-nesting community, cavities are the central resource, and PCEs, WCEs and SCNs represent different levels of a hierarchy (Martin and Eadie 1999). Based on the number and strength of the links within a food web, a variety of predictions about community stability, diversity and resiliency have been derived (e.g., Pimm 1980; Warren 1990; Cohen et al. 1990; Waltho and Kolasa 1994; de Ruiter et al. 1995). Food web theory is well developed, and being able to apply it to cavity-nesting communities, at Eglin and

elsewhere, promises to provide new understanding of the structure and functioning of these communities.

The goal of this study is to characterize the links of one species, the RCW, with other members of the cavity-nesting community at Eglin through both correlational and experimental methods. Links may be direct or indirect, weak or strong, and positive or negative. Relationships within the cavity-nesting community at Eglin, particularly those involving RCWs, are especially intriguing for two reasons. First, as discussed above, there are concerns about impacts of RCW management on other species, and about impacts of other species on this endangered species. Second, RCWs may have exceptionally numerous and strong links with other cavity-nesting species due to peculiarities of the longleaf pine ecosystem. Among PCEs only the RCW can excavate cavities in live pine trees, and within the fire-maintained longleaf system the snags and hardwoods in which other PCEs excavate are not always widely available (Allen 2001; Conner et al. 2001). As a result, many species normally considered PCEs may function instead as WCEs in this system, using RCW cavities as well as excavating their own. In a preliminary study we detected nests of seven other species in cavities originally excavated by RCWs on Eglin. Three of these were SCNs (American kestrel; eastern screech owl *Otus asio*; wood duck *Aix sponsa*). The other four, however, were woodpecker species that elsewhere are PCNs (red-bellied woodpecker *Melanerpes carolinus*; red-headed woodpecker *M. erythrocephalus*; northern flicker *Colaptes auratus*; pileated woodpecker *Dryocopus pileatus*).

We measured the abundance and nest cavity use of members of the cavity-nesting community on Eglin in areas with and without RCWs, and related abundance to numbers of RCWs, numbers of cavities excavated by RCWs and numbers of snags. We further examined these relationships by experimentally increasing and reducing cavity availability. In conducting these activities we distinguished between normal cavities and enlarged cavities. Many of the cavity-nesting species cannot use RCW cavities unless they have been enlarged by other woodpeckers, and RCWs will no longer use cavities that have been enlarged substantially. Thus the process of enlargement creates a potential for indirect interactions between RCWs and larger SCNs, mediated by other woodpecker species.

Objectives

1. To measure the abundance of red-cockaded woodpeckers and other cavity-nesting species, as well as abundance of potential nest sites (RCW cavities and snags) and nests on replicate plots.
2. To describe the relationships of the variables described in (1) through correlational analysis.
3. To experimentally alter availability of red-cockaded woodpecker cavities and measure resulting changes in abundance and nests of other cavity-nesting species.

Methods

Field Methods

Eglin Air Force Base encompasses 187,555 hectares, much of which consists of longleaf pine sandhills and flatwoods communities. Sandhill communities alone occupy 78% of the land area (DOD 1999). Thus the base is uniquely suited to large-scale studies

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that require replicate plots within longleaf communities, such as our previous experiment (Walters et al. 2002a) and the study by Provencher et al. (2001). Especially important to the design of our study is the existence of areas of longleaf sandhills in which RCWs no longer occur, which enabled us to avoid confounding of treatment (i.e., RCW density) with habitat.

We established 36, 800x600-meter plots for the cavity-nesting community study in areas of variable red-cockaded woodpecker density (Figure 11). Plots were restricted to the Sandhills Ecological Association and were selected to represent typical RCW habitat. Plots contained up to 43 RCW cavities, and 12 plots contained no RCW cavities. We employed a large plot size to accommodate the large territorial scale of many woodpecker species in the study system. Other factors besides density of RCW cavities considered in plot selection included the presence of old-growth longleaf pine, lack of clear-cuts, plantations and major roads and variation in snag density.

In each plot, we established a grid system to aid with general navigation during nest searching, relocation of nests and distance estimation (Figure 12). The grid system within each plot consisted of nine 600-meter transects located 100 meters apart, with each transect flagged at 50m intervals for visibility. We placed metal poles in the ground at 100m intervals along transects to maintain a permanent plot setup over the duration of the study. We ensured transect distance accuracy by setting up each plot with the use of a Trimble sub-meter global positioning system (GPS) unit. Due to landscape constraints, some plots were oriented north-south, while others were oriented east-west. We established 12 point-count census stations within each plot, with three stations located on each of four alternating transects (Figure 12). Census stations were located at least 200m apart and were treated as sub-samples within each plot. Each plot was an experimental sampling unit.

We recorded the relative abundance (detections/survey) of cavity-nesting birds at all censusing stations within each plot twice annually between April and July 2002-2005. We measured abundance using a modified point count/transect count censusing technique, which was adapted for the open, pine savannah habitat (Provencher et al 2002). We conducted censuses on two plots (24 census stations) per morning, within the first three hours after sunrise, and recorded species, species location, time detected, vocalization type and sex. We recorded species detections by distance class (0-25m, 25-50m, 50-75m, 75-100m). Due to the open midstory and high detectability of some of the larger cavity-nesting species, it was easy to detect certain birds beyond 100m. We truncated detections beyond 100m in the direction of plot edges to ensure that birds off the plot were not counted.
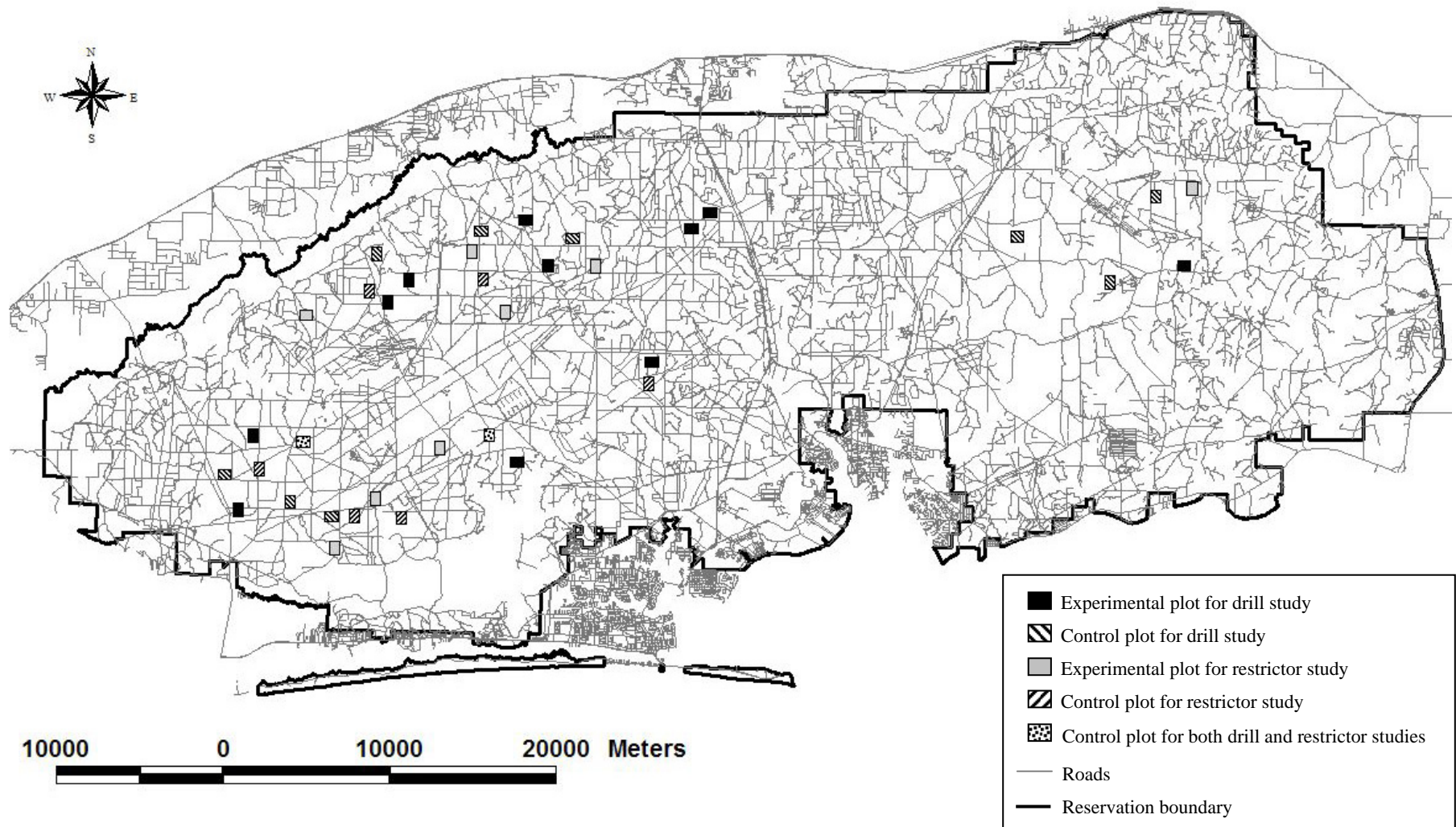
Figure 11. Location of 36 plots used in the cavity-nester study, including 22 used for the cavity-drilling experiment (11 treatment, 11 control) and 16 for the cavity-restrictor experiment (8 treatment, 8 control). Note that two plots are used as control plots for both experiments.
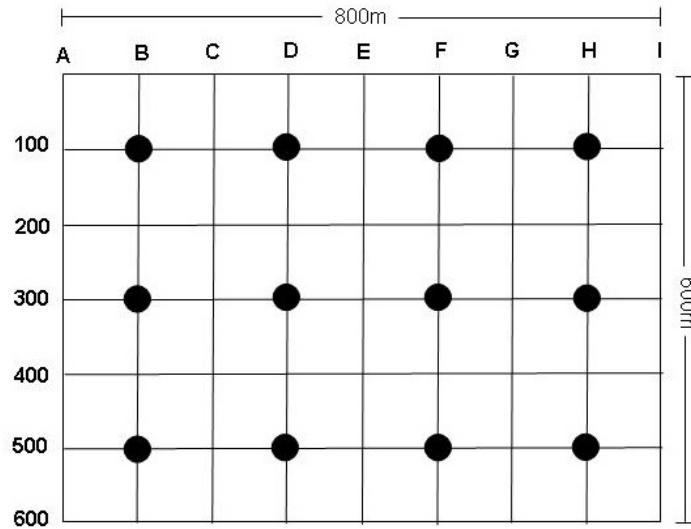
Figure 12. Diagram showing the layout of the research plots used in the cavity-nester study. On each plot, nine transects (labeled A-I), each 600m in length, were spaced 100m apart. Twelve census stations were located on alternating transects, spaced 200m apart (indicated by the black circles).

We minimized double-counting within each plot by censusing simultaneously with two observers (i.e. one observer each on adjacent transects), synchronizing start-times for the eight-minute point counts using hand-held radios. We included birds detected along transects between census stations in the counts. This transect-count addition to the point-count censusing provided an opportunity to account for fleeing (or quiet) birds not detected due to the confines of point count methodology. Additionally, transect counts provide improved ability to detect birds in open habitat (Bibby et al 1992) and to detect uncommon species (Hutto et al. 1986). After returning from the field sampling, we compared the results of both observers for all stations within each plot, thus mapping the bird detections over the entire plot area. Because starting times were synchronized, we were able to identify detections of birds by the two observers that had matching location, times and vocalization type. In these cases, we removed one record from the census.

For each species and each round of censusing, we calculated relative abundance by summing the total number of individuals detected at all 12 census stations in a plot. We used the maximum number of detections for the plot (across the two sampling rounds) as the measure of abundance for that season. In their study at Eglin AFB, Provencher et al (2002) compared this modified point/transect count method to standard point count methodology and found no substantial difference between the two methods, except for reduced variability in detection rates using the modified point/transect method.

We also recorded abundance of non-cavity nesters to assess confounding between treatment and habitat condition (Martin and Eadie 1999). We defined two sets of non-cavity nesting birds based on their association with hardwood midstory, a characteristic reflective of good or poor quality RCW habitat. Non-cavity nesting species associated with an open midstory (NonCavOpen) included Bachman's sparrow (*Aimophila aestivalis*), northern bobwhite (*Colinus virginianus*) and loggerhead shrike (*Lanius ludovicianus*). Non-cavity nesting species associated with a developing hardwood/shrub

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midstory (NonCavMidstory) include northern cardinal (*Cardinalis cardinalis*), Carolina wren (*Thryothorus ludovicianus*) and eastern towhee (*Pipilo erythrophthalmus*). A positive association of the NonCavOpen group with RCW cavities and snag availability would indicate confounding of good habitat quality and cavity availability.

We conducted nest searching twice in each plot annually between April and the end of July, 2002 through 2005. In 2002, nest searching was exploratory and used to develop a systematic protocol for the remainder of the study. Systematic nest searching began in 2003 and continued through 2005. Nest searching consisted of two parts: one crew focused only on cavity-nests in non-RCW cavity trees (e.g., snags) and another crew focused on nests in RCW cavities. The latter crew systematically inspected the contents of all RCW cavities within each plot twice each field season. Observers recorded the status (i.e., normal/enlarged, active/inactive) of all RCW cavities inspected. The former crew searched each plot twice for snag-nests per season. Each member of the snag-nest crew spent a total of 6 hours nest-searching in each plot, totaling 12 person-hours per plot for the season. Observers located nests by walking along transects in each plot and inspecting all snags for potential nest cavities. Observers also located cavity nests by observing bird behavior and by checking tagged nest trees from previous years. Both crews inspected cavities using a Sandpiper Technologies Treetop Peeper, which consists of a camera mounted atop an extendable fiberglass utility pole.

We tagged all nest trees and monitored nests to determine number of eggs, nestlings and fledglings. We used the number of nestlings recorded approximately one week prior to projected fledging date as the number of fledglings and classified nests that contained at least one fledgling as successful.

The order in which plots were censused and searched for nests was determined randomly within each of the two rounds of sampling, and then on the basis of obtaining access to restricted areas of the Eglin reservation. We rotated the starting order and observer assignment to transect within a plot across plot visits in order to minimize observer biases in bird and nest detectability. We only conducted censuses and nest searching under satisfactory weather conditions: good visibility, little or no precipitation and light winds (Martin 1997).

Each year, after completing censusing and nest searching, we collected data on all snags located within 25m of each point count station. Snags were defined as dead, standing trees $\geq$ 10.2cm dbh and $\geq$ 1.4m tall. We classified snags into type (pine/hardwood) and structural class based on branching, bark and general level of decay (Table 7). We calculated snag availability for each plot by summing data across all 12 sampling stations per plot per year. We found no nests in class 1 snags (Table 7), presumably because the wood in such snags is not sufficiently decayed for excavation. Therefore we excluded class 1 snags from calculations of snag availability within each plot. We documented the number of old-growth (flattop) longleaf within 25m of each point count station as well, however we collected these data only the first year since the number of old-growth longleaf pine changes relatively little from year to year. We measured longleaf flattop abundance to control for habitat quality, in case presence of old-growth trees affected bird abundance.

From November 2003 through January 2005, we experimentally manipulated the availability of normal-sized and enlarged RCW cavities through cavity drilling and application of cavity restrictors. We selected 11 plots, each originally containing 0-5

(mean = 1.8) living RCW cavity trees, for cavity addition. We designated 11 additional plots containing 0-7 (mean = 2.2) RCW cavity trees as controls. We selected experimental and control groups to have a comparable range of snag densities. In each of the experimental plots, we drilled approximately 12 RCW cavities, depending on availability of drillable trees. We constructed a total of 130 cavities, resulting in a range of 11-20 cavities (mean = 13.8) per plot. We designated a different set of 8 plots as experimental plots for the restrictor study, along with 8 control plots. In order to obtain 8 control plots for this part of the study, we reused two of the control plots from the cavity addition experiment. Both experimental and control groups contained enlarged RCW cavities and a comparable range of snag densities. In each experimental plot, we restricted the entrance diameter of all inactive and/or enlarged RCW cavities to 2" using metal restrictor plates, restricting 135 cavities in total. We completed the experimental manipulations just prior to the 2005 field season. Because the systematic protocol for nest searching began in 2003, and experimental treatments were completed after the 2004 field season, the experimental portion of this study consists of 2003 data (pre-treatment) and 2005 data (post-treatment).

Table 7. Structural classification system for snags.

Snag Class	Description
1	Recently dead trees, most bark, branches and crown intact
2	Dead several years, >50% bark and branches intact, top sometimes broken
3	Dead several years, <50% bark and branches intact, top usually broken
4	Long dead, no branches or bark, broken top, extensive decay

Statistical Analyses

In all analyses we employed SAS System 9.1 and a significance level of $P < 0.05$, and because the data were non-normally distributed, we used nonparametric statistics. For the observational portion of the study (2002-2003), we applied a Spearman's partial correlation analysis to the abundance data to determine the correlations of species with one another, with density of class 2-4 snags (Table 7) and with number of RCW cavities, controlling for the effects of old-growth pine. We computed correlations to pine and oak snags separately. For these analyses we calculated mean detections per plot for each species, pooled across both years, and used these values as our data points. To compute snag densities (snags/ha), we averaged the number of snags per 25-m radius sampling station per plot and divided by sampling station area (0.196ha). To test for confounding of habitat quality with cavity availability, we correlated abundance of the two non-cavity nesting bird assemblages (Non CavOpen and NonCavMidstory) with number of RCW cavities, pine snags and hardwood snags. To compare census and nest searching results, we correlated mean detections per plot with mean number of nests per plot for each species. Finally, we incorporated both abundance data and nest data from 2002-2003 into web diagrams to provide a visual depiction of community structure among cavity-nesting birds on Eglin.

For the experimental analyses, to control for annual variation in the data, we tested for a treatment effect by comparing the amount of change in bird and nest abundance between 2003 and 2005 in treatment and control plots. That is, for each plot we subtracted the pre-treatment values from the post-treatment values and used the differences for analysis in a nonparametric, paired t-test (Wilcoxon rank sum-Mann

Whitney U). Because our a priori predictions were directional, we used one-tailed tests in these analyses.

Many of the focal species in this study have large territory sizes and thus, we found relatively few nests per species within each plot. Additionally, many species nested in large pine snags, which were relatively abundant in many of the plots, thus reducing the sample of nests found in RCW cavities. Due to the small sample size of nests found, we grouped species together into 1) those that enlarge or use enlarged cavities (LCN), 2) those that use unaltered RCW cavities (NCN) and 3) those that do not use RCW cavities (OCN). We analyzed effects of the treatments on RCWs separately. For sake of comparison, we analyzed abundance data at both the species and group levels.

Results and Discussion

Census Results

We detected 52 bird species, including 14 cavity-nesters that breed in Eglin, during the censuses from 2002-2005 (Table 8). We recorded an additional secondary cavity nester, the purple martin (*Progne subis*), but do not consider it a breeding bird on Eglin. The purple martin occurs in the Florida panhandle but is not known to breed in longleaf pine forests, and we found no nests of this species during the four years of this study. The purple martin now breeds almost entirely in man-made birdhouses except for a few regions east of the Rocky Mountains (Brown 1997).

Table 8. Bird species detected during point counts from April through July, 2002-2005. Obligate cavity-nesters that breed on Eglin are indicated with an asterisk.

Species	Scientific Name	Abbreviation
Breeding Birds		
American crow	*Corvus brachyrhyncho*	AMCR
Southeastern American kestrel*	*Falco sparverius paulus*	AMKE
Bachman's sparrow	*Aimophila aestivalis*	BACS
Barn swallow	*Hirundo rustica*	BARS
Black vulture	*Coragyps atratus*	BLVU
Blue grosbeak	*Guiraca caerulea*	BLGR
Blue-gray gnatcatcher	*Polioptila caerulea*	BGGN
Blue-jay	*Cyanocitta cristata*	BLJA
Broad-winged hawk	*Buteo platypterus*	BWHA
Brown thrasher	*Taxostoma rufum*	BRTH
Brown-headed nuthatch*	*Sitta pusilla*	BHNU
Carolina chickadee*	*Parus carolinensis*	CACH
Carolina wren	*Thryothorus ludovici*	CARW
Chimney swift	*Chaetura pelagica*	CHSW
Chuck-will's-widow	*Caprimulgus caroline*	CWWI
Common grackle	*Quiscalus quiscula*	COGR
Common nighthawk	*Chordeiles minor*	CONI
Common yellowthroat	*Geothlypis trichas*	COYE

Coopers hawk	*Accipiter cooperii*	COHA
Downy woodpecker*	*Picoides pubescens*	DOWO
Eastern bluebird*	*Sialia sialis*	EABL
Eastern kingbird	*Tyrannus tyrannus*	EAKI
Eastern meadowlark	*Sturnella magna*	EAME
Eastern screech owl*	*Otus asio*	EASO
Eastern towhee	*Pipilo erythrophthal*	EATO
Eastern tufted titmouse*	*Parus bicolor*	ETTI
Fish crow	*Corvus ossifragus*	FICR
Great-crested flycatcher*	*Myiarchus crinitus*	GCFL
Great-horned owl	*Bubo virginianus*	GHOW
Hairy woodpecker*	*Picoides villosus*	HAWO
Indigo bunting	*Passerina cyanea*	INBU
Loggerhead shrike	*Lanius ludovicianus*	LOSH
Mississippi kite	*Ictinia mississippienis*	MIKI
Mourning dove	*Zenaida macroura*	MODO
Northern bobwhite	*Colinus virginianus*	NOBO
Northern cardinal	*Cardinalis cardinalis*	NOCA
Northern flicker*	*Colaptes auratus*	NOFL
Northern mockingbird	*Mimus polyglottos*	NOMO
Northern rough-winged swallow	*Stelgidopteryx serripennis*	NRWS
Pileated woodpecker*	*Dryocopus pileatus*	PIWO
Pine warbler	*Dendroica pinus*	PIWA
Purple martin	*Progne subis*	PUMA
Red-bellied woodpecker*	*Melanerpes carolinus*	RBWO
Red-cockaded woodpecker*	*Picoides borealis*	RCWO
Red-eyed vireo	*Vireo olivaceus*	REVI
Red-headed woodpecker*	*Melanerpes erythrocephalus*	RHWO
Red-shouldered hawk	*Buteo linneatus*	RSHA
Red-tailed hawk	*Buteo jamaicensis*	RTHA
Summer tanager	*Piranga rubra*	SUTA
Turkey vulture	*Cathartes aura*	TUVU
White-eyed vireo	*Vireo griseus*	WEVI
Wild turkey	*Meleagris gallopavo*	WITU
Yellow-billed cuckoo	*Coccyzus americanus*	YBCU

Migrants
American goldfinch	*Carduelis tristis*	AMGO
Cedar waxwing	*Bombycilla cedrorum*	CEDW
Chipping sparrow	*Spizella passerina*	CHSP

House wren	*Troglodytes aedon*	HOWR
Tree swallow	*Tachycineta bicolor*	TRES
Yellow-bellied sapsucker	*Sphyrapicus varius*	YBSA
Yellow-rumped warbler	*Dendroica coronata*	YRWA

Uncommon Sightings (1-2 times over the 4-year period)

Eastern wood pewee	*Contopus virens*	EAWP
Gray catbird	*Dumetella carolinensis*	GRCA
Hooded warbler	*Wilsonia citrina*	HOWA
House finch	*Carpodacus mexicanus*	HOFI
Northern parula	*Parula americana*	NOPA
Orchard Oriole	*Icterus spurius*	OROR
Palm warbler	*Dendroica palmarum*	PAWA
Prairie warbler	*Dendroica discolor*	PRWA
Ruby-crowned kinglet	*Regulus calendula*	RCKI
Ruby-throated hummingbird	*Archilochus colubris*	RTHU
Veery	*Catharus fuscescens*	VEER
Yellow-breasted chat	*Icteria virens*	YBCH
Yellow-throated vireo	*Vireo flavifrons*	YTVI

Correlations in abundance between cavity nesting birds, based on abundance data from 2002 and 2003, are shown in Table 9. Correlations between each cavity nesting bird species and various cavity resources (pine snags, hardwood snags and RCW cavities) are shown in Table 10. Five cavity-nesting birds were positively and significantly correlated with RCW cavities on Eglin, including the RCW itself, and in addition the southeastern American kestrel, brown-headed nuthatch, northern flicker and red-headed woodpecker. The American kestrel, northern flicker and red-headed woodpecker were positively and significantly correlated with pine snags. The red-bellied woodpecker was correlated with one class (class 3, Table 7) of pine snags. Five species were positively and significantly correlated with hardwood snags, including the red-bellied woodpecker, eastern tufted titmouse, Carolina chickadee, great-crested flycatcher and downy woodpecker.

Neither of the non-cavity nesting bird groups (NonCavOpen or NonCavMidstory) were significantly correlated with RCW cavities ($p=0.69$ and $p=0.52$ respectively) or with hardwood snags ($p=0.10$ and $p=0.54$, respectively). Both non-cavity nesting bird groups were positively correlated (only one significantly) with pine snags ($p=0.09$ and $p=0.05$, respectively). These results indicate that there is no significant confounding of habitat quality with cavity resource availability within plots in our data.

Table 9. Spearman partial correlation between cavity nesting birds based on abundance data from all 36 plots from April-July 2002 and 2003, pooled across years (n=72). In the matrix, the upper value is the correlation coefficient (r) and the lower value is the significance level (p). Species abbreviations are provided in Table 8.

	AMKE	BHNU	CACH	DOWO	EABL	GCFL	HAWO	NOFL	PIWO	RBWO	RCWO	RHWO	ETTI
AMKE	1.00	0.42	-0.09	-0.04	0.05	-0.19	0.10	0.42	0.08	0.03	0.41	0.39	-0.18
		0.00	0.48	0.48	0.69	0.12	0.38	<0.01	0.50	0.81	<0.01	<0.01	0.13
BHNU		1.00	-0.09	-0.01	0.31	-0.24	0.11	0.41	-0.06	-0.00	0.48	0.37	-0.26
			0.43	0.95	0.01	0.04	0.35	<0.01	0.64	0.98	<0.0001	<0.01	0.03
CACH			1.00	0.25	0.06	0.56	0.06	0.09	0.14	0.33	-0.31	-0.06	0.49
				0.03	0.64	<0.0001	0.61	0.45	0.25	<0.01	0.01	0.61	<0.0001
DOWO				1.00	0.12	0.35	0.07	0.11	0.19	0.12	-0.12	0.13	0.23
					0.33	<0.01	0.57	0.35	0.11	0.32	0.31	0.28	0.05
EABL					1.00	-0.10	-0.05	0.13	-0.08	-0.13	0.09	0.02	-0.17
						0.39	0.70	0.29	0.48	0.28	0.48	0.86	0.16
GCFL						1.00	-0.07	-0.00	0.27	0.38	-0.24	-0.06	0.55
							0.56	0.98	0.02	<0.01	0.04	0.62	<0.0001
HAWO							1.00	-0.00	0.32	0.11	-0.05	-0.15	-0.03
								0.97	0.01	0.37	0.65	0.19	0.78
NOFL								1.00	0.12	0.17	0.11	0.45	-0.10
									0.32	0.16	0.36	<0.0001	0.39
PIWO									1.00	0.07	-0.19	-0.04	0.15
										0.58	0.12	0.77	0.20
RBWO										1.00	-0.04	0.26	0.33
											0.76	0.03	0.01
RCWO											1.00	0.39	-0.30
												<0.01	0.01
RHWO												1.00	-0.16
													0.19
ETTI													1.00

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Table 10. Spearman partial correlation between cavity nesters and cavity resources, including longleaf pine snags (Longleaf Snags), hardwood snags (Hardwood Snags) and red-cockaded woodpecker cavities (RCWO Cavities) based on census and snag data from all 36 plots from April-July 2002 and 2003, pooled across years (n=72). In the matrix, the upper value is the correlation coefficient (r) and the lower value is the significance level (p). Species abbreviations are provided in Table 8.

	AMKE	BHNU	CACH	DOWO	EABL	GCFL	HAWO	NOFL	PIWO	RBWO	RCWO	RHWO	ETTI
# Longleaf Snags	0.43	0.14	0.23	-0.06	-0.06	-0.04	-0.14	0.24	-0.00	0.09	0.19	0.42	0.03
	<0.001	0.24	0.06	0.62	0.61	0.76	0.25	0.05	0.98	0.46	0.12	<0.001	0.83
# Hardwood Snags	0.02	-0.12	0.28	0.31	0.05	0.31	0.06	0.01	0.10	0.29	-0.19	0.07	0.27
	0.88	0.31	0.02	<0.01	0.68	<0.01	0.62	0.94	0.42	0.01	0.12	0.59	0.02
RCWO Cavities	0.50	0.37	-0.18	-0.04	-0.07	-0.12	-0.05	0.31	-0.17	0.01	0.73	0.36	-0.28
	<0.0001	<0.01	0.12	0.76	0.55	0.33	0.67	<0.01	0.17	0.93	<0.0001	<0.01	0.02

Cavity Nests

Between 2002 and 2005, we found 866 nests of the 14 species of cavity-nesting birds (Table 11). The total includes reuse of the same cavity across years, but not re-nesting attempts within the same year. Nests found outside of the research plots (n=134, typically within 50m) are also included in these data, since they provide an increased sample from which to obtain information on nest characteristics. Nests found outside of the research plots, however, are excluded from analysis in the experimental portion of the study, since plot is the experimental unit. The majority of nests were found in pine snags (excluding dead RCW cavity trees) (n=508, 59%). The second most common resource used by cavity nesters was the living RCW cavity tree (n=227, 26%), followed by hardwood snags (n=89, 10%) and then dead RCW cavity trees (n=42, 5%). Excluding RCW nests, which are exclusive to living pine, the distribution of cavity nests for all other species was 68% in pine snags, 15% in live RCW cavity trees, 12% in hardwood snags and 6% in dead RCW cavity trees. These numbers are heavily influenced by the red-headed woodpecker, which was the most abundant cavity nester detected in this study (36% of nests found) and used, almost exclusively, pine snags with very little bark. The sizes (mean dbh) of the snags, both pine and hardwood, used for nesting by cavity-nesting species on Eglin are shown in Figure 13, and nest heights for these species are shown in Figure 14. The figures do not include RCWs since they always nested in live pines rather than snags.

Table 11. Cavity nests found between April and July, 2002-2005 on the 36 plots, in pine and hardwood snags, and live and dead RCW cavity trees (RCW Trees).

	SNAGS (non-RCW)		RCW Trees		Total Nests Found
	Pine	Hardwood	Live	Dead	
Southeastern American kestrel	96	2	38	27	163
Brown-headed nuthatch	2	4	0	0	6
Carolina chickadee	0	4	0	0	4
Downy woodpecker	0	10	0	0	10
Eastern bluebird	1	3	1	0	5
Eastern screech owl	14	11	27	3	55
Eastern tufted titmouse	2	7	0	0	9
Great-crested flycatcher	1	1	0	0	2
Hairy woodpecker	0	6	0	0	6
Northern flicker	59	13	14	6	92
Pileated woodpecker	4	0	2	0	6
Red-bellied woodpecker	33	28	21	1	83
Red-cockaded woodpecker	0	0	115	0	115
Red-headed woodpecker	296	0	9	5	310
Total	508	89	227	42	866

Figure 13. Mean diameter at breast height (cm) of pine and hardwood snags used for nesting by cavity-nesting species, 2005-2005. Bars include standard error. Data are based on 488 nests (403 pine, 85 hardwood), and do not include cases of re-use of the same nest tree by the same species or nests in snags whose dbh could not be measured due to fire damage. Species abbreviations are given in Table 8.
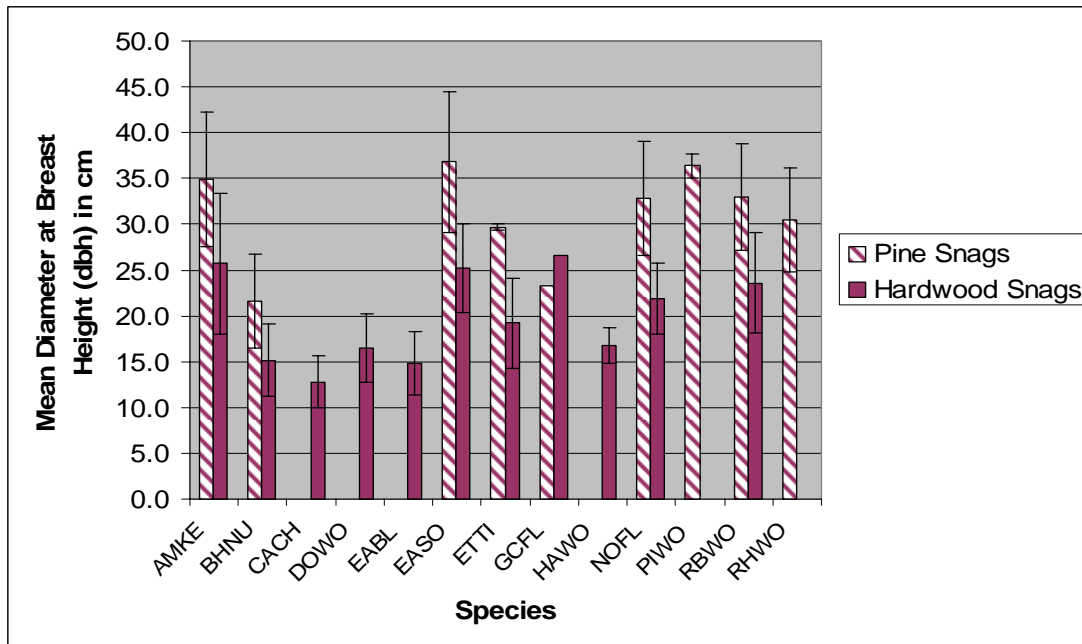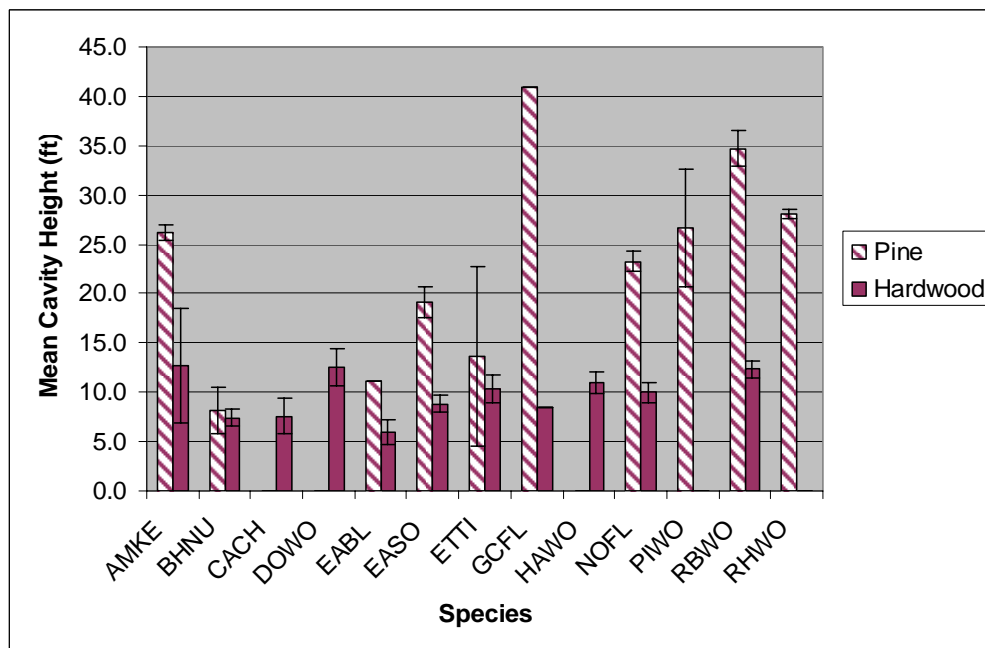

Figure 14. Mean height (ft) of cavities in pine and hardwood snags used for nesting by cavity-nesting species, 2005-2005. Bars include standard error. Data are based on 606 nests (518 pine, 88 hardwood), and do not include reuse of the same cavity by the same species. Species abbreviations are given in Table 8.

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Abundance Webs and Nest Webs

We incorporated the abundance data from 2002-2003 into a web diagram, based on the correlations of the abundance of each species to RCW cavities, pine snags, hardwood snags and other cavity-nesters (Figure 15). In the abundance web, one group contains those species that were correlated with pine snags and a second group those correlated with hardwood snags. Because all five species in the pine web (red-headed and red-cockaded woodpeckers, northern flicker, brown-headed nuthatch and southeastern American kestrel) were also positively and significantly correlated with RCW cavities, RCW cavity trees are included in the pine web. Members of the hardwood web include the eastern tufted titmouse, Carolina chickadee, red-bellied woodpecker, downy woodpecker and great-crested flycatcher. One species, the red-bellied woodpecker, is positively correlated to both hardwood snags and one type of pine snags (class 3, Table 7) and thus connects the hardwood and pine webs (Figure 15). The eastern screech owl was not detected using our censusing methodology and therefore was not included in the abundance web. Three other cavity-nesting species (eastern bluebird, pileated woodpecker and hairy woodpecker) were not significantly correlated with pine snags, hardwood snags or RCW cavity trees and hence were not part of the abundance webs.

We incorporated nest data from 2002 and 2003 into three nest web diagrams, following Martin and Eadie (1999) and Martin et al (2004). The webs are divided into several levels including primary cavity excavators (PCE), weak excavators (WCE), secondary cavity nesters (SCN) and trees. Nest webs include all nests for which we could identify the species responsible for excavating the cavity (n=424). When we could not identify the excavator, either through known use of the cavity or reasonable estimation based on typical cavity characteristics, we excluded the nests from the web. Figure 16 indicates nest resource use by the cavity-nesting bird community at Eglin. All links in this web reflect the proportion of nests found in the connecting resource. A link connecting a SCN to a PCE is interpreted as the proportion of that SCN's nests found in cavities originally excavated by the connected PCE. A link connecting a PCE to the tree level is interpreted as the proportion of that PCE's nests found in the connected tree type. Alternatively, Figure 17 indicates cavity excavation within this system, rather then nest use. In this figure a link between a PCE and a tree is interpreted as the proportion of total nests found (of any species) that were originally excavated by that PCE in the connected tree resource type. Note that cavity nests found in dead RCW cavity trees were originally excavated by RCWs into a living pine, and are reflected accordingly in the excavation web.

In Figure 18 we partition the nest web data into pine and hardwood groups to facilitate comparison with the abundance web (Figure 12). In Figure 18, links between the SCN-PCE levels reflect proportion of the SCN's nests found in a cavity excavated by the connected PCE. However, links between the PCE and Tree levels reflect the proportion of total nest cavities (of any species) excavated by the PCE in the various connected tree resources. The Carolina chickadee is not shown in the nest web, since we found no nests of this species in 2002 or 2003. Additionally, although we found one eastern bluebird nest in 2003, we were unable to identify the excavator of the cavity and thus had to exclude it from the nest web diagrams.

48
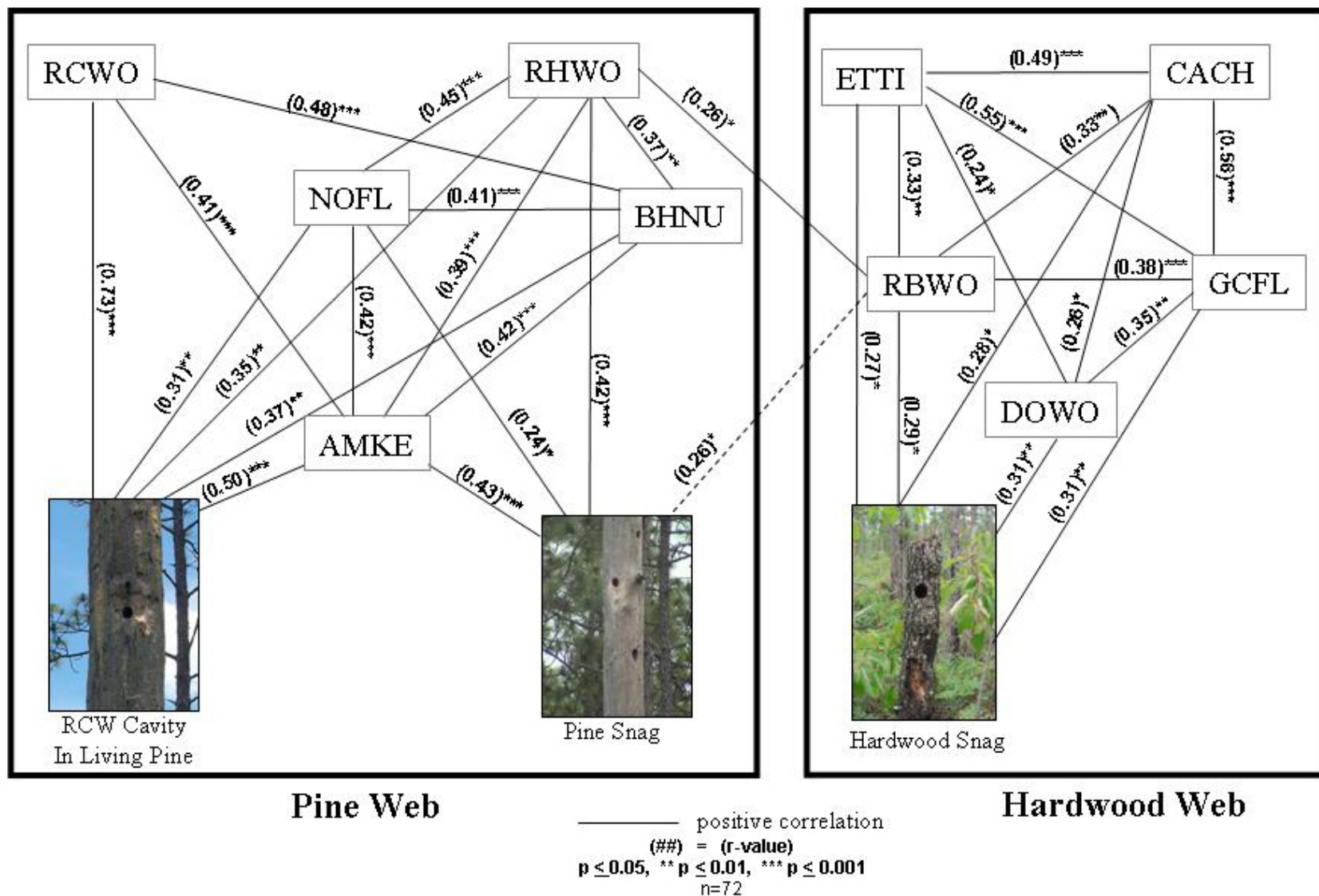
Figure 15. Bird-abundance web based on census data from 2002 and 2003, pooled across both years. Numbers represent Spearman's partial correlation coefficients (r), controlling for the effect of old-growth pine on bird abundance. The eastern screech owl is not shown in the webs because it was not detected using our census methodology. Only species that showed a significant correlation with a cavity resource are included in the web. Bird species abbreviations are given in Table 8.

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Figure 16. Nest web diagram of the cavity nesting bird community. N indicates the number of nests found for that species, E the total number of nesting cavities excavated by that species. Links between the Secondary Cavity Nester (SCN) level and the Primary Excavator (PCE) level represent the proportion of the SCN's nests found in a cavity excavated by the indicated PCE. Links between the PCE and Tree levels reflect the proportion of PCE nests found in the indicated tree resource. The link between the northern flicker and the red-headed woodpecker indicates that 2% of flicker nests were found in cavities originally excavated by a red-headed woodpecker.

50
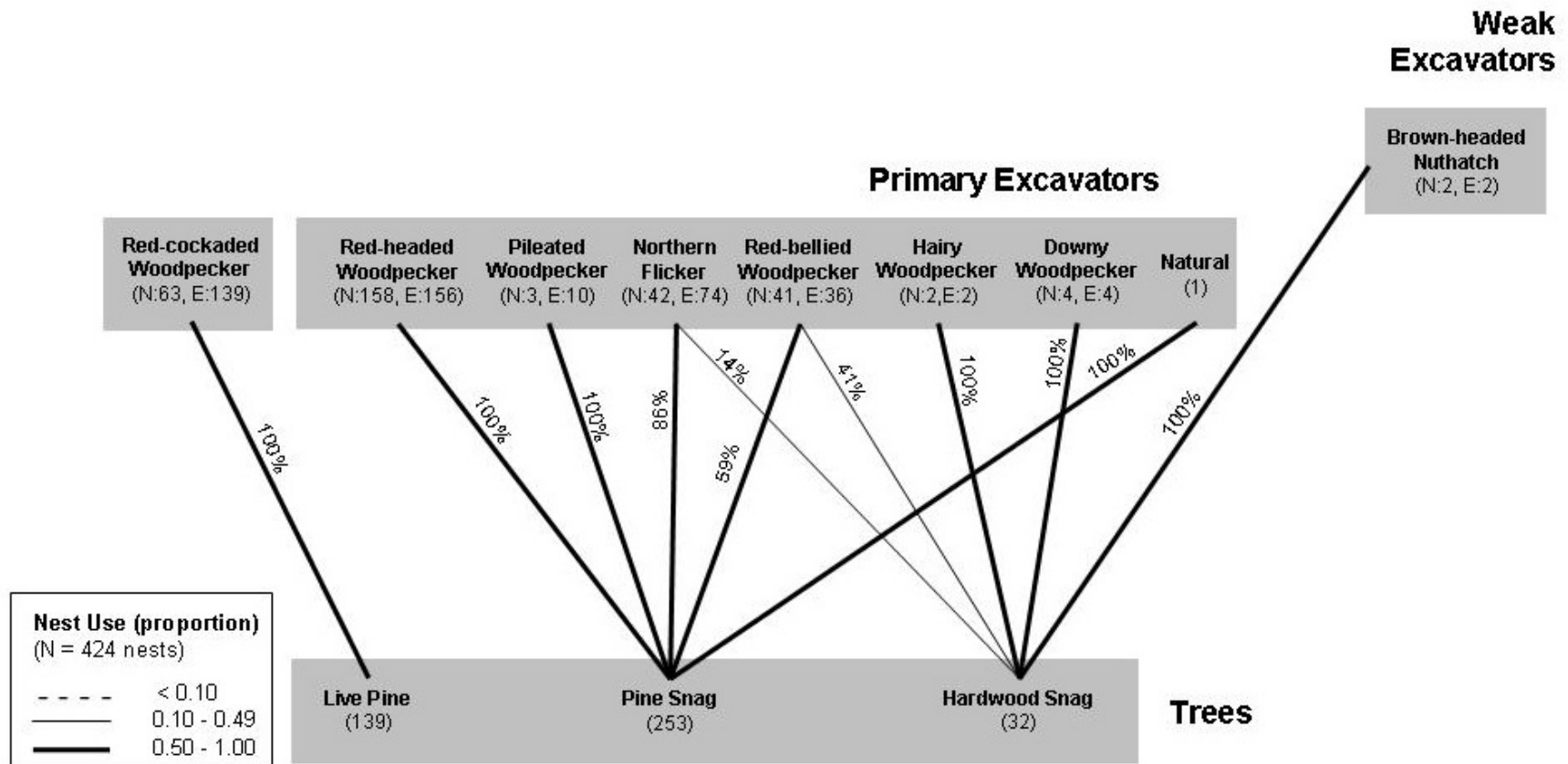
Figure 17. Cavity excavation web diagram of the cavity nesting bird community. N indicates the number of nests found for that species, E the total number of nesting cavities excavated by that species. Li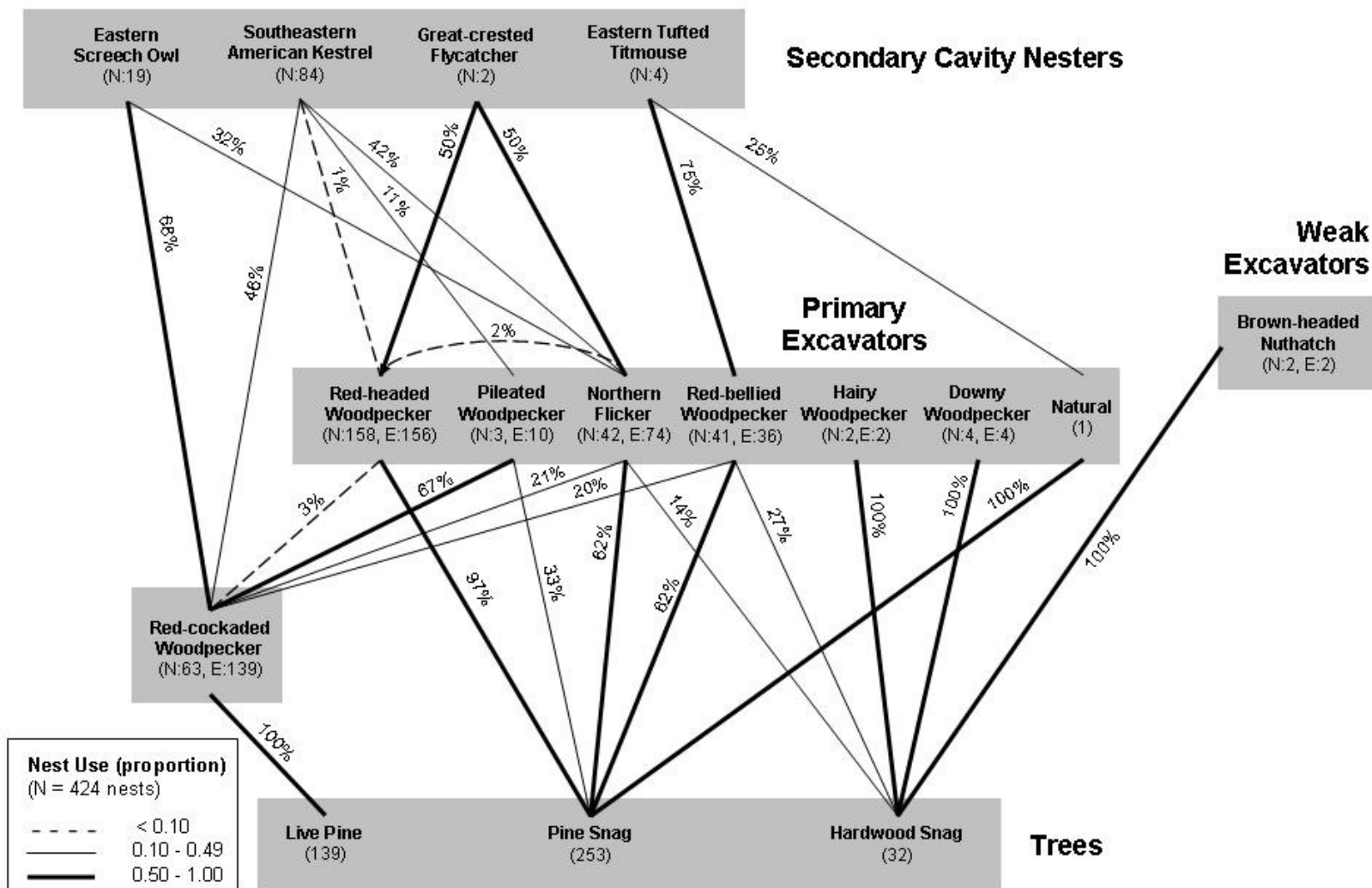nks between a Primary Excavator (PCE) and the Tree levels reflect the proportion of nesting cavities excavated by that particular PCE in the tree resource.
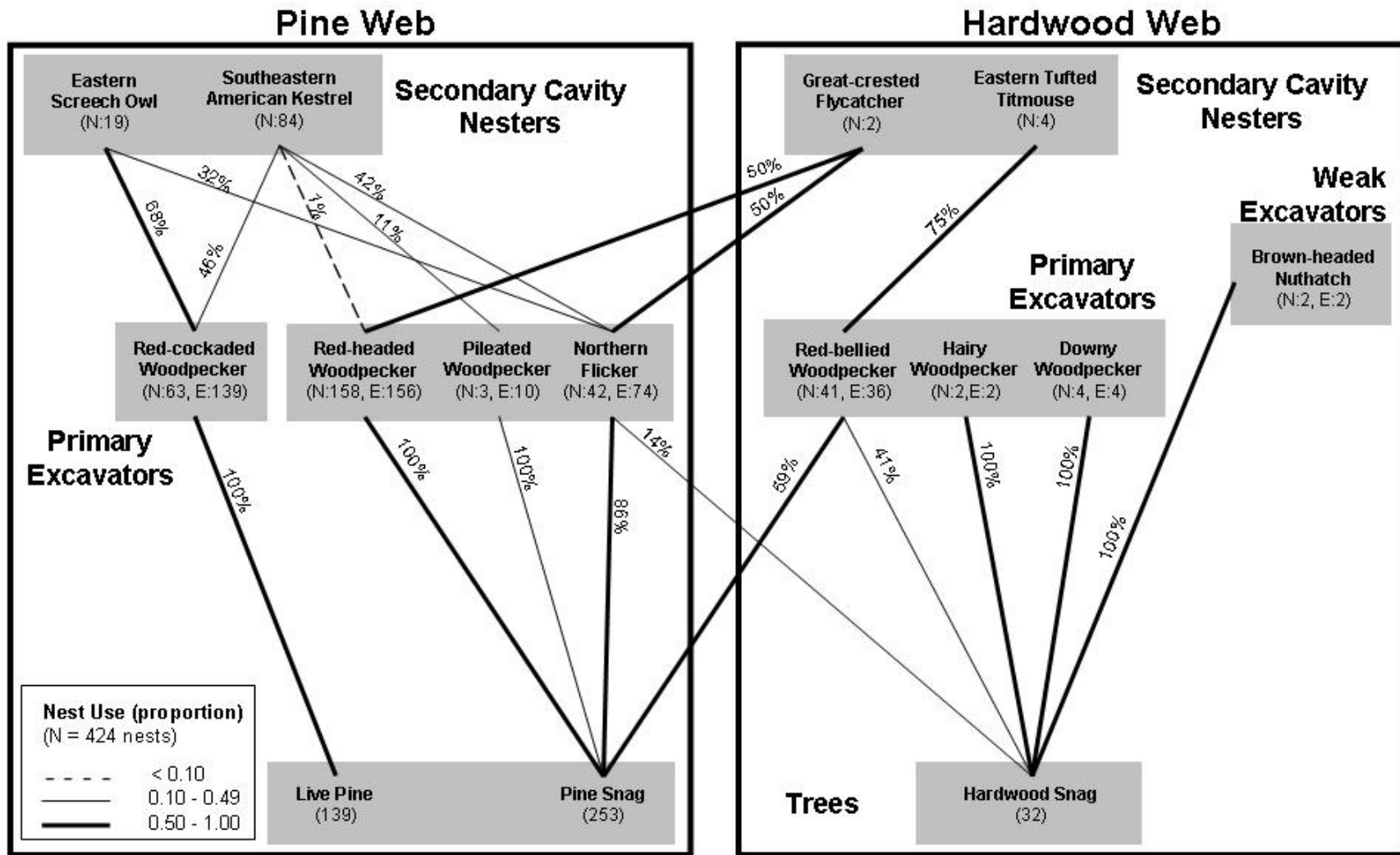
Figure 18. Nest web diagram of the cavity nesting bird community, created for comparison to the abundance web shown in Figure 15, which is partitioned into pine and hardwood groups. N indicates the number of nests found for that species, E the total number of nesting cavities excavated by that species. Links between Secondary Cavity Nesters (SCN) and Primary Excavators (PCE) indicate the proportion of that SCN's nests found in cavities excavated by the PCE. Links between a PCE and the Tree level reflect the proportion of nesting cavities excavated by that particular PCE in the tree resource.

Abundance webs and nest webs serve as complementary depictions of cavity-nesting bird community structure on Eglin. They differ primarily in their depiction of species that are easy to detect but whose nests we rarely found (e.g., Carolina chickadee), or that are difficult to detect but whose nests are readily found (e.g., eastern screech owl). Taken together, the abundance and nest data suggest there are two core groups of cavity-nesting birds in the sandhill communities on Eglin, 1) those species associated primarily with pine snags and RCW cavity trees and 2) those associated with hardwood snags. Based on nesting data, the most abundant species in the cavity-nesting community on Eglin include the red-headed woodpecker, southeastern American kestrel, red-cockaded woodpecker, northern flicker, red-bellied woodpecker, and eastern screech owl. These species account for the majority of nests found during our study. The northern flicker was the primary creator of large cavities, which are required for nesting by secondary cavity-nesters such as the southeastern American kestrel and eastern screech owl. While pileated woodpeckers were detected in our censuses, their abundance, number of nests and number of cavities excavated were relatively low compared to other species in this system. This is probably due to their large territory size. Our nest data suggest that the RCW and northern flicker provide the most cavities for other species in this system, relative to their nesting abundance. RCW nests accounted for 15% of the nests found, but their cavities accounted for 33% of nests found. Northern flicker nests accounted for 10% of nests found, but their cavities accounted for 18% of nests found. The red-headed woodpecker was the most prolific cavity excavator, but use of its cavities by other species was rare.

Large pine snags and RCW cavity trees are the primary nesting resources for cavity-nesting birds on Eglin. Overall snag densities (including class 1 snags) on the study plots are shown in Table 12, and densities by size class are shown in Table 13. It is evident from these data that large pine snags are abundant on Eglin. This is no doubt due to a moratorium on removal of live or dead longleaf pine, combined with the unusually high abundance (compared to elsewhere in the Southeast) of large, old-growth longleaf on the reservation. Large pine snags were actually even more numerous than is at first evident in Table 13. Snags whose dbh could not be measured because the lower portion of the tree was burnt to the heartwood (Figure 19) were always large enough to accommodate cavity nests, and often were large enough to accommodate the largest SCNs such as the southeastern American kestrel. In fact 17% of the nests we found in pine snags (n=549) were in such trees, including 22 kestrel nests, 14 flicker nests, and 48 red-headed woodpecker nests. These snags constitute the 0 dbh size class in Table 13. We contend that these snags fall in the 25-49.9cm, further increasing the already high densities of such snags.

Table 12. Snag densities (mean number of snags/ha) on the 36 study plots during the four years of the cavity-nester study. Standard errors are shown in parentheses.

	2002	2003	2004	2005
Hardwood	13.9 (0.87)	15.5 (1.67)	10.6 (0.89)	10.5 (0.98)
Pine	7.9 (0.63)	8.0 (0.65)	5.2 (0.43)	5.2 (0.45)
Total	21.8 (1.05)	23.5 (1.76)	15.8 (0.96)	15.7 (1.10)

The abundance of snags on Eglin, in particular large, mature longleaf snags, likely has a major influence on the dynamics of Eglin's cavity-nesting bird community (Gault et al. 2004). These snags are not common in other southeastern pine forests due to current forest management practices, which include harvesting pine snags for timber. Low availability of large snags appears to increase use of RCW cavities by other species. For example, at many sites in the

Southeast usurpation of RCW cavities by red-headed woodpeckers is common (e.g., North Carolina Sandhills, Everhart et al. 1993; Appalachicola National Forest, E. Walters 2004; Camp Blanding Training Site and Goethe State Forest, Kappes 2004). In contrast, we rarely observed use of RCW cavities by red-headed woodpeckers: only 9 of 321 nests (3%) of the red-headed woodpeckers we found on Eglin between 2002 and 2005 were in RCW cavities. These findings suggest that the abundance of snags at Eglin may reduce the dependency of other cavity nesting birds on RCW cavities and ultimately ease cavity usurpation pressure on the RCW.

Table 13. Snag densities on Eglin, by dbh size class, compared to recommended densities for Florida from McComb et al. (1986). All densities are mean number of snags per 40ha. Annual values for Eglin are means across the 432 sampling stations within the 36 cavity-nester study plots. The 0cm class is comprised of trees whose dbh could not be measured due to fire damage.

	Recommended for Florida	Eglin			
		2002	2003	2004	2005
0 cm	n/a	60.38	156.60	79.71	110.85
10.2-12.6cm	n/a	216.98	201.88	148.58	140.56
12.7-24.9cm	120	449.05	427.82	313.20	284.43
25-49.9cm	84	143.39	123.58	92.92	89.15
>50	8	1.88	1.42	0.94	0.47
Total > 12.7cm	212	594.33	552.82	407.07	374.05

Figure 19. Two longleaf pine snags with unmeasurable diameter at breast height due to fire damage.

Snag availability on Eglin greatly exceeds the recommended guidelines proposed for Florida by McComb et al. (1986) (Table 13). The mortality of old-growth pine resulting from prescribed fire that we contend above is detrimental to RCWs is responsible in part for the high densities of large snags we observed. As such mortality is reduced due to improvements in burning techniques and reduced fuel loads snag availability likely will decline. Indeed it is evident from Tables 12 and 13 that this is already occurring. If our interpretation of the dynamics of the cavity-nesting community is correct, as snag availability declines, use of RCW cavities by other species will increase. There is some indication that this, too is beginning to occur: the number of red-bellied and red-headed woodpecker nests found in RCW cavities increased from two in 2002 to 11 in 2005. Increased usurpation of cavities, which at worst can occasionally interfere with nesting, has much less impact on RCW population dynamics than loss of cavity trees to fire, which can cause territory abandonment. Therefore our findings from the cavity-nester study do not cause us to alter our recommendation to reduce losses of RCW cavity trees to prescribed fire. Even if such losses were eliminated, there would still be sufficient pine mortality due to other, natural causes to maintain an adequate supply of pine snags for other cavity-nesting species, as long as large pine snags continue to be retained on the landscape.

Experimental Study

We found 391 cavity nests in all plots in 2003 (pre-treatment) and 2005 (post-treatment) combined, including cavity nests in both snags and live RCW cavity trees. Data are shown in Tables 14 and 15 by bird size grouping (LCN, NCN, OCN and RCW), nest resource (live RCW cavity tree versus snag) and treatment.

As predicted, there was a significantly greater increase in both abundance (Z=-1.71, p=0.04) and in number of nests (Z=-2.25, p=0.02) of RCWs on the experimental plots relative to control plots following addition of cavities (Figures 20 and 21). There was no difference between the change in LCN (Z=.-0.67, p=0.25) or OCN (Z=0.30, p=0.38) abundance on experimental plots and control plots following addition of cavities (Figure 20). The change in NCN abundance was marginally significantly different between experimental and control plots (Z=-1.46, p=0.07), influenced heavily by the red-headed woodpecker (Z=-2.16, p=0.02; Table 16), with control plots showing a larger decline than plots to which cavities were added. There was no significant difference between experimental and control plots in the change in number of nests following addition of cavities for the LCN, NCN or OCN groups (Figure 21).

Table 14. Nests found in 2003 and 2005 on 22 plots in the cavity addition experiment. Data are shown by bird size grouping (LCN, NCN, OCN and RCW) and nest resource (live RCW cavity tree vs. snag) for both control and experimental (Drill) plots. The LCN group includes those species known to use enlarged RCW cavities; NCN includes those species that used normal-sized RCW cavities; OCN include other cavity-nesters that do not use RCW cavities.

Group	Treatment	Nests in RCW Cavities (2003)	Nests in RCW Cavities (2005)	Nests in Snags (2003)	Nests in Snags (2005)	% Nests RCW Cavities (2003)	% Nests RCW Cavities (2005)	% Nests Snags (2003)	% Nests Snags (2005)
LCN	Control	2	4	19	20	9.5%	16.7%	90.5%	83.3%
LCN	Drill	0	3	14	12	0.0%	20.0%	100.0%	80.0%
NCN	Control	0	0	34	25	0.0%	0.0%	100.0%	100.0%
NCN	Drill	0	1	29	32	0.0%	3.0%	100.0%	97.0%
OCN	Control	0	0	2	4	0.0%	0.0%	100.0%	100.0%
OCN	Drill	0	0	2	3	0.0%	0.0%	100.0%	100.0%
RCW	Control	3	2	0	0	100.0%	100.0%	0.0%	0.0%
RCW	Drill	2	6	0	0	100.0%	100.0%	0.0%	0.0%

Table 15. Nests found in 2003 and 2005 on 16 plots in the cavity restrictor experiment. Data are shown by bird size grouping (LCN, NCN, OCN and RCW) and nest resource (live RCW cavity tree vs. snag) for both control and experimental (Restrict) plots.

Group	Treatment	Nests in RCW Cavities (2003)	Nests in RCW Cavities (2005)	Nests in Snags (2003)	Nests in Snags (2005)	% Nests RCW Cavities (2003)	% Nests RCW Cavities (2005)	% Nests Snags (2003)	% Nests Snags (2005)
LCN	Control	5	9	16	9	23.8%	50.0%	76.2%	50.0%
LCN	Restrict	11	2	10	13	52.4%	13.3%	47.6%	86.7%
NCN	Control	2	4	25	12	7.4%	25.0%	92.6%	75.0%
NCN	Restrict	2	2	24	11	7.7%	15.4%	92.3%	84.6%
OCN	Control	0	0	2	3	0.0%	0.0%	100.0%	100.0%
OCN	Restrict	0	0	0	3	0.0%	0.0%	0.0%	100.0%
RCW	Control	5	7	0	0	100.0%	100.0%	0.0%	0.0%
RCW	Restrict	12	8	0	0	100.0%	100.0%	0.0%	0.0%
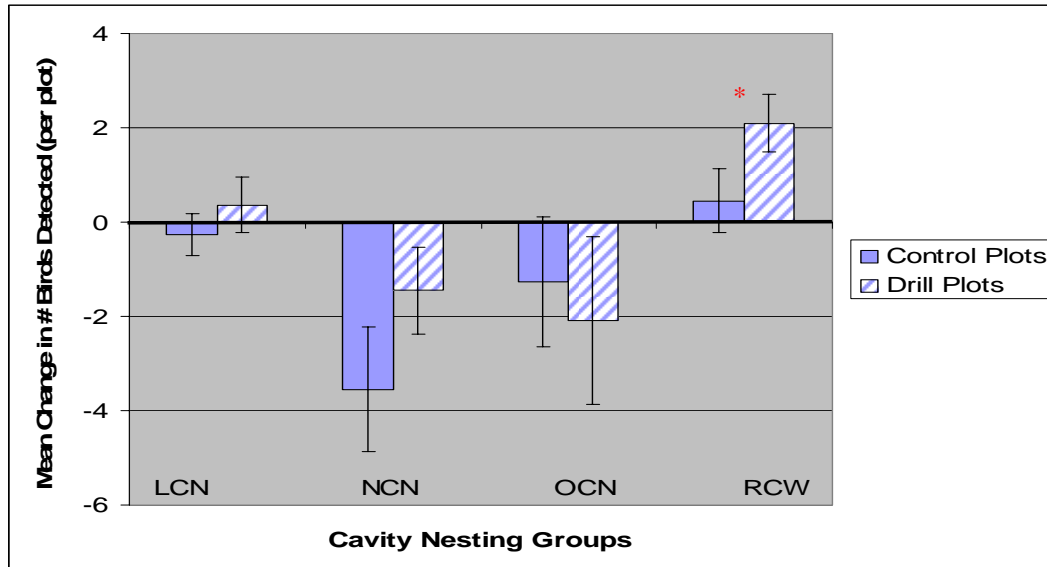
Figure 20. Changes in the relative abundance of cavity nesting birds in response to addition of artificial cavities for RCWs, on control and experimental (drill) plots. Bars reflect the mean change in relative abundance from 2003 to 2005, including standard error. LCN are those species known to use enlarged RCW cavities, NCN those species that use normal-sized RCW cavities and OCN other cavity-nesters that do not use RCW cavities. An asterisk indicates a significant difference between control and experimental plots.

Figure 21. Changes in the number of nests found in RCW cavities in control and experimental (drill) plots following addition of artificial cavities. Bars reflect the mean change in the number of nests found from 2003 to 2005, including standard error. LCN are those species known to use enlarged RCW cavities, NCN those species that use normal-sized RCW cavities and OCN other cavity-nesters that do not use RCW cavities. An asterisk indicates a significant difference ($p<0.05$) between control and experimental plots.

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Table 16. Changes in relative abundance in experimental (drill) and control plots from 2003 to 2005 following addition of artificial cavities. Z-values and significance levels (p) for differences between treatments using the nonparametric Wilcoxon Rank Sum Test (Mann-Whitney U) are indicated (n=22). Standard error is shown in parentheses after the means.

Species	Mean Change (Drill Plots)	Mean Change (Control Plots)	Z-value	p
Southeastern American kestrel	0.73 (0.36)	-0.18 (0.38)	-1.360	0.09
Brown-headed nuthatch	-0.45 (0.61)	-0.27 (0.76)	0.399	0.35
Carolina chickadee	-0.64 (0.89)	0.00 (0.67)	0.101	0.46
Downy woodpecker	0.09 (0.37)	0.09 (0.34)	-0.106	0.46
Eastern bluebird	-0.64 (0.49)	-0.55 (0.31)	-0.238	0.41
Great-crested flycatcher	0.09 (0.48)	0.00 (0.36)	-0.384	0.35
Eastern tufted titmouse	-1.27 (0.76)	-0.73 (0.80)	0.398	0.35
Hairy woodpecker	0.09 (0.16)	-0.36 (0.20)	-1.593	0.06
Northern flicker	0.09 (0.34)	0.09 (0.39)	-0.030	0.49
Pileated woodpecker	-0.45 (0.16)	-0.18 (0.23)	0.800	0.21
Red-bellied woodpecker	-1.09 (0.65)	-1.18 (0.96)	-0.100	0.46
Red-cockaded woodpecker	2.09 (0.61)	0.45 (0.68)	-1.700	0.04
Red-headed woodpecker	0.27 (0.60)	-1.82 (0.60)	-2.160	0.02

There was no difference between the change in LCN (Z=0.43, p=0.34), OCN (Z=-0.37, p=0.36) or RCW (Z=-1.07, p=0.14) abundance in experimental and control plots following addition of cavity restrictors (Figure 22). The change in NCN abundance was marginally significant (Z=-1.54, p=0.06), influenced heavily by the eastern bluebird (Z=-2.08, p=0.02; Table 17), with abundance declining more on control plots than experimental plots following treatment. For nest data, however, there was a significant difference between control and experimental plots for LCN (Z=2.72, p=0.003). Specifically, in experimental plots, there was a reduction in the number of LCN nests found in RCW cavities (Figure 23) and an increase in LCN nests found in snags (Figure 24) following application of cavity restrictors (Z=-1.82, p=0.03). The increase in LCN snag nests in experimental plots contrasted with a decrease in LCN snag nests in control plots. There was no difference between experimental and control plots in changes in number of nests of NCN (Z=0.54, p=0.29) or OCN (Z=0, p=0.5) following treatment, primarily because few to no nests of these groups were found in RCW cavity trees. Interestingly, there was a marginally significant reduction in RCW nests in experimental plots relative to controls following application of restrictors (Z=1.62, p=0.10) (Figure 23), even though RCW abundance showed the opposite trend (Figure 22).
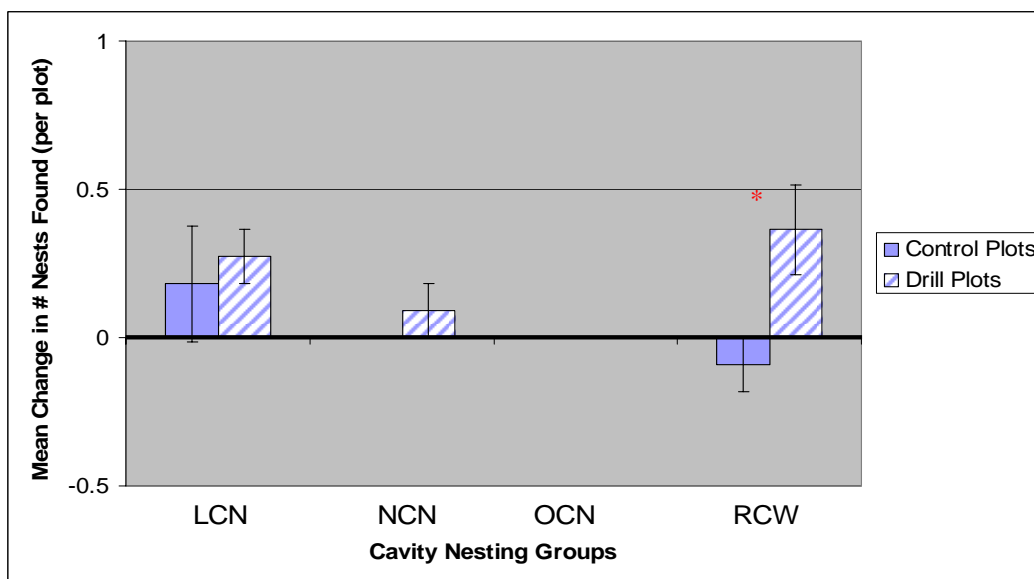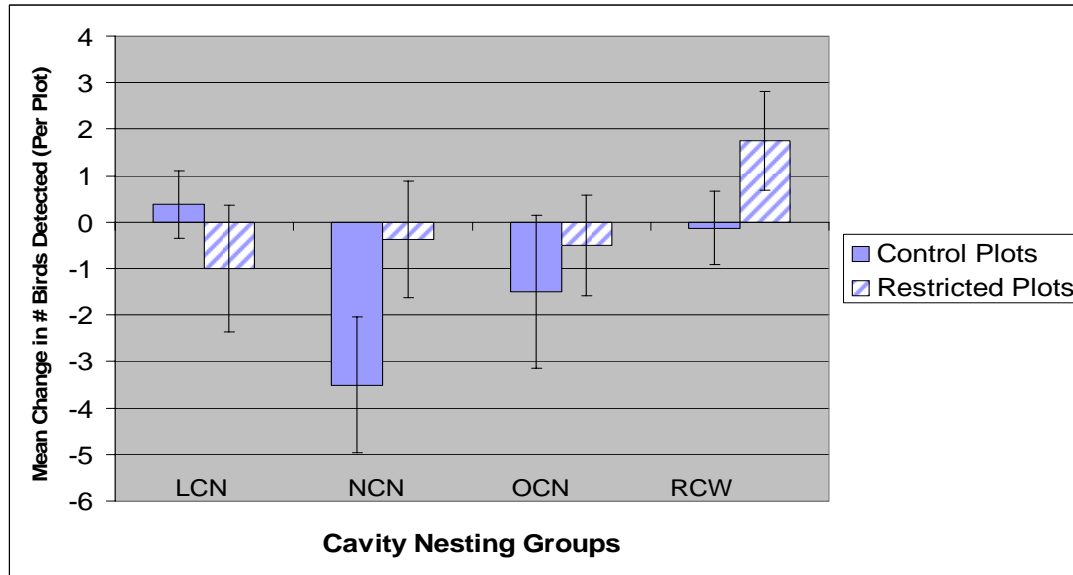
Figure 22. Changes in the relative abundance of cavity nesting birds in response to restricting RCW cavities. Bars reflect the mean change in relative abundance from 2003 to 2005, including standard error, for both control and experimental (Restricted) plots, following application of restrictors. None of the differences shown were statistically significant (p=0.05).

Table 17. Changes in species abundance in experimental (Restrict) and control plots from 2003 to 2005, following application of cavity restrictors. Z-values and significance levels (p) for differences between treatments using the nonparametric Wilcoxon Rank Sum Test (Mann-Whitney U) are indicated (n=16). Standard error is shown in parentheses after the means.

Species	Mean Change (Restrict Plots)	Mean Change (Control Plots)	Z-value	p-value
Southeastern American kestrel	-1.375 (1.27)	-0.5 (0.46)	0.321	0.37
Brown-headed nuthatch	0.75 (0.80)	1.13 (0.91)	0.213	0.42
Carolina chickadee	-0.25 (0.41)	-0.88 (0.55)	-0.828	0.20
Downy woodpecker	0.13 (0.30)	-0.63 (0.32)	-1.408	0.08
Eastern bluebird	0.38 (0.32)	-0.88 (0.40)	-2.084	0.02
Eastern tufted titmouse	-0.88 (0.23)	-1.00 (0.63)	0.734	0.23
Great-crested flycatcher	-0.13 (0.23)	0.25 (0.25)	1.055	0.156
Hairy woodpecker	-0.13 (0.23)	-0.38 (0.26)	-0.449	0.33
Northern flicker	0.38 (0.71)	0.63 (0.56)	0.325	0.37
Pileated woodpecker	0.0 (0.0)	0.25 (0.25)	1.040	0.15
Red-bellied woodpecker	-0.63 (1.13)	-1.38 (0.84)	-0.214	0.42
Red-cockaded woodpecker	1.75 (1.06)	-0.13 (0.79)	-1.068	0.14
Red-headed woodpecker	-0.13 (0.67)	-1.25 (0.86)	-1.220	0.11

Figure 23. Changes in the number of nests found in RCW cavities in control and experimental (Restrict) plots from 2003 to 2005, following application of cavity restrictors. Bars reflect the mean change, including standard error. An asterisk indicates a significant difference (p<0.05) between control and experimental plots.
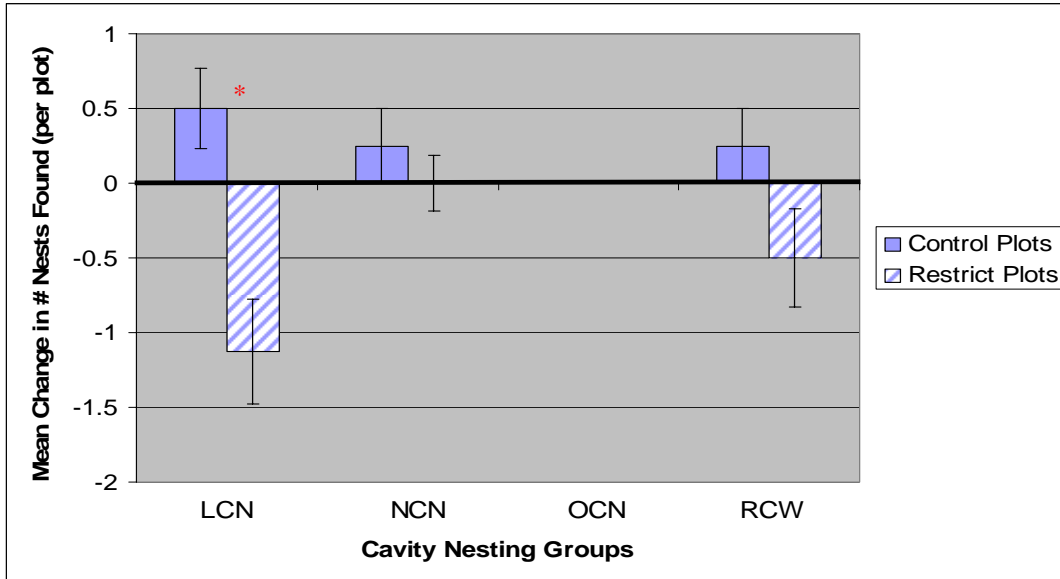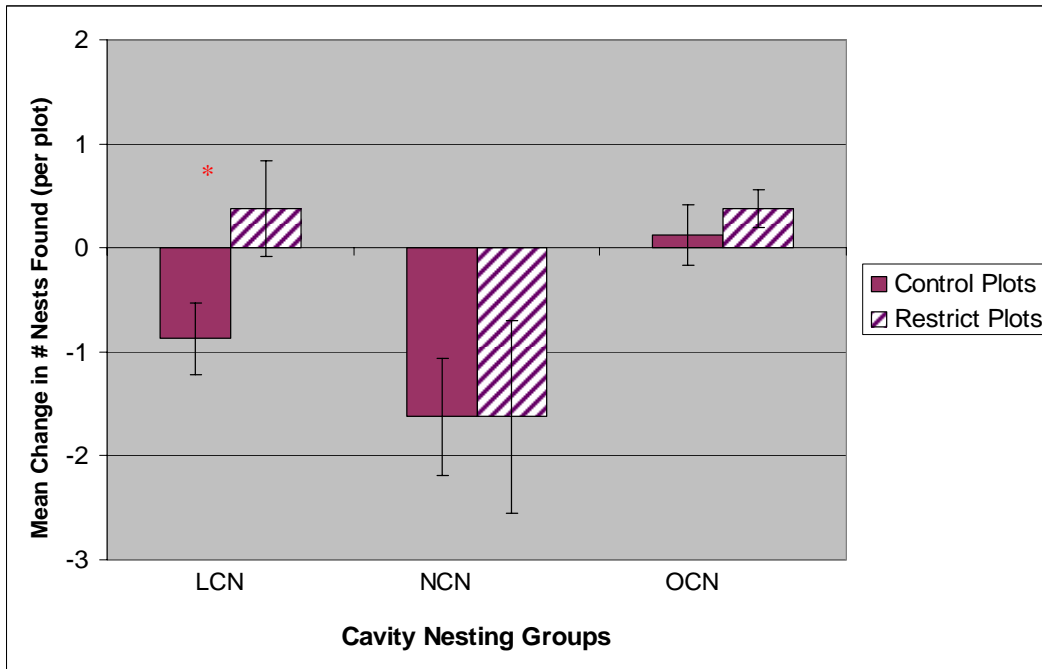

Figure 24. Changes in the number of cavity nests found in snags in control and experimental (Restrict) plots from 2003 to 2005, following application of cavity restrictors. Bars reflect the mean change, including standard error. An asterisk indicates a significant difference (p<0.05) between control and experimental plots.

The abundance and nest webs from the observational portion of the study suggested interactions between species that were tested in the experimental portion of the study. The experiments provided some evidence of strong interactions, but results, being based on only one year of observation post-treatment, were equivocal in some cases. Drilling cavities in living pine trees had a clear effect on the species that excavates such cavities, the RCW, resulting in an increase in both abundance and nests. The only other species affected was the red-headed woodpecker, the abundance of which decreased in control plots but not in plots to which cavities were added. One possible explanation of this result is that RCW cavities provide a stabilizing alternative to variation in snag availability from year to year. By August 2005, 25% of the newly drilled cavities had RCW activity, 9% were showing signs of cavity enlargement and one contained a red-headed woodpecker nest. These data suggest that larger responses to the treatment may occur eventually, and that the time scale of the current study was too short to see the full effects of the manipulation. Response times to manipulations in terrestrial systems often take many years (Power et al. 1996). Therefore we hope to resample the plots again in 2010.

The experimental results suggest that the use of metal restrictor plates on RCW cavities can have negative impacts on large cavity nesters, including the southeastern American kestrel, eastern screech owl and northern flicker. These impacts, however, appear to be mitigated by the availability of snags, especially large pine snags, on the landscape. Large pine snags and RCW cavity trees are the primary nesting resources for this group of birds and both resources were relatively abundant at Eglin during the years this study was conducted. Accordingly, large cavity nesting birds were able to switch to using snags in experimental plots where RCW cavities were restricted and thus, their abundance was not affected. Forcing large cavity nesters to switch to different, possibly lower-quality nesting sites, could potentially result in a reduction in reproductive success. One small SCN, the eastern bluebird, showed a response to the restrictor treatment similar to the response of red-headed woodpeckers to the cavity drilling treatment: eastern bluebird abundance decreased in control plots, but not in the restrictor plots. It is possible that preventing large cavity nesters from using enlarged RCW cavities increased availability of these cavities to eastern bluebirds. However, given that no eastern bluebird nests were found in restricted RCW cavities in 2005, this explanation seems unlikely.

An interesting and unexpected result in the restrictor experiment was a marginally significant decrease in RCW nests in plots with restrictors relative to control plots. Because RCW abundance actually increased slightly in the restrictor plots, it is unclear whether the reduction in nests found was a spurious result or a genuine response to the treatment. Restrictors were applied only to enlarged and inactive RCW cavities. It is possible that restricting RCW cavities may cause other cavity-nesters to switch to unrestricted cavities in the area, thereby reducing the number of unrestricted cavities available to RCWs.

Conclusions

We achieved our objectives of measuring and describing the community of cavity nesting birds on Eglin, and at least began the process of testing the identity and strength of direct and indirect interactions between species by observing responses of the community to experimental manipulations. The results of our study suggest that the RCW can indirectly and positively affect large cavity nesting birds through cavity excavation, mediated by other woodpecker species, notably the northern flicker. This raises the possibility that restricting cavities to benefit RCWs could have negative effects on other species. Of particular concern is the southeastern American kestrel, which has a strong, positive and significant correlation to RCW cavities and

was affected by the use of restrictor plates. The kestrel depends on other cavity-excavating birds to provide nesting cavities and has declined by 82% since the early 1940's (McFarlane 1973, Hoffman and Collopy 1988). It is listed as threatened in Florida, and the population on Eglin appears to be one of the largest and most productive remaining in the state (Gault et al. 2004). On Eglin, not only RCW cavities but also large pine snags are an important nesting resource for kestrels. We recommend that restrictor plates be used sparingly and in combination with retention of large pine snags on the landscape in order to provide for not only southeastern American kestrels, but also the other large SCNs in the community, the eastern screech owl. Snag retention could potentially reduce usurpation pressure on the RCW by providing alternate nesting sites for other cavity-nesting species.

There is no indication of any negative impacts on any other species of providing artificial cavities for RCWs. The observational portion of our study suggested there may be positive effects of cavity provisioning on several other species, including not only the large SCNs but other PCEs (Figure 16). The experimental portion of the study did not reveal any strong short-term effects of cavity provisioning on these species, but long-term effects are likely. We suggest five years as an appropriate interval over which long-term effects might emerge, and thus recommend resampling the plots in 2010.

The study yielded several surprising results, including the importance of the northern flicker as a source of cavities for large SCNs, through both its own excavations and its enlargement of RCW cavities, the contrasting lack of importance of the pileated woodpecker in this same role, and the weakness of the direct interactions of RCWs with red-headed and red-bellied woodpeckers. The northern flicker has been shown to play an important and similar role in other cavity-nesting communities (Moore 1995; Martin and Eadie 1999; Saab et al. 2004; Martin et al. 2004), but that this role extends to the longleaf pine community was previously unappreciated. In other locations pileated woodpeckers enlarge many RCW cavities, often severely damaging them (Saenz et al. 1998), to the point that they are considered a serious threat to RCWs (Walters 1991; USFWS 2003). This does not appear to be a significant problem on Eglin. Similarly, negative interactions of RCWs with red-headed and red-bellied woodpeckers, best characterized as cavity kleptoparasitism (Kappes 1997), appear to be less frequent at Eglin than elsewhere. We have proposed that this is due to the fact that red-headed and red-bellied woodpeckers are more dependent on RCW cavities in other areas than they are at Eglin, where the presence of large pine snags provides an alternative nesting resource for these species. Others have suggested that retention of large pine snags on the landscape might benefit RCWs by reducing cavity kleptoparasitism (Rudolph et al. 1990; Kappes and Harris 1995). The presence of numerous large pine snags makes Eglin unique among longleaf pine communities today. Documenting the role of these snags in and importance to the cavity-nesting bird community is one of the most important results of our study. The dynamics of the cavity-nesting bird community on Eglin can be used as a baseline for comparison to communities elsewhere where the absence of large, old-growth snags imposes stress on the relationships between species and presumably increases competition between them. The nest webs documented on Eglin provide a context for examining direct and indirect interactions between species, including those involving the RCW, elsewhere.

The cavity-nester study constitutes the Ph.D. dissertation research of one of the graduate students supported by the project, Lori Blanc. In addition to the results presented in this report, Ms. Blanc's completed dissertation will include path modeling of interactions between cavity-

nesting bird species at Eglin, based on cavity resource-use. Ms. Blanc's dissertation will be submitted to Eglin as an additional product of the project when it is completed in May 2007.

POPULATION STUDIES OF AMPHIBIANS
Background

Amphibians have been identified as a focus for conservation with increasing frequency in recent years. Amphibians are thought to be useful as "indicator" species because their permeable skin and anamniotic eggs make them sensitive to many types of disturbance and because their complex life cycles integrate effects of disturbances in terrestrial and aquatic systems. With a recent focus on global declines in amphibian populations (Wake 1991; Pechmann and Wilbur 1994; Halliday 1998), and with a greater understanding of the important role of amphibians in ecosystem processes (Burton and Likens 1975a; 1975b; Pough et al. 1987; Wake 1991), land managers increasingly are being asked to maintain and restore populations of amphibians.

For many species of amphibians little information exists about demography or natural history, such as habitat requirements at different life stages, and almost none about response to land management practices. In recent years, however, numerous studies of the effects of forest management practices on amphibian populations have been conducted, primarily on populations of terrestrial salamanders (Bennett et al. 1980; Pough et al. 1987; Ash 1988; 1997; Petranka et al. 1993; 1994; Chazal and Niewiarowski 1998; DeMaynadier and Hunter 1998; Harpole and Haas 1999; Herbeck and Larsen 1999; Grialou et al. 2000; Hanlin et al. 2000). Still, little information exists about such potential problems as the effects of fire suppression or prescribed fires (but see Russell et al. 1999), plantation forestry including ditching and bedding, or road construction and increased traffic volume on existing roads (Means et al. 1996; Gibbs 1998).

Eglin is home to a diverse suite of amphibians and reptiles including the federally threatened (64 FR 15691-15704) flatwoods salamander and the endemic Florida bog frog listed as a state species of special concern (Florida Fish and Wildlife Conservation Commission 1997). The flatwoods salamander occurs primarily in longleaf pine savannas (Ashton 1992; Palis 1996) and its populations have apparently declined with the loss of this habitat (Means et al. 1996; Palis 1996). The Florida bog frog, not described until 1985, is a highly restricted endemic, occurring only on the base and its immediate surroundings, and thus is limited to three counties (Okaloosa, Santa Rosa, and Walton counties) of Florida (Moler 1993).

In this study we undertook collection of data on distribution and habitat requirements of these two species in order to improve Eglin's ability to manage for them on the base. Because so little is known about the natural history and demography of these species, it is difficult to predict the effects of habitat management or military training activities on their populations. Although it appears clear that regular fire is important to both species and that soil or hydrologic disturbance has negative effects, there is no information about the scale of disturbance to which these species might respond. Understanding the importance of habitat management at different distances from aquatic breeding sites will be necessary to devise effective management.

In particular our goal was to evaluate current distribution, population size, and turnover of Florida bog frogs, and for flatwoods salamanders, to assess the effects of surrounding land use characteristics on larval density in ponds and collect more detailed demographic information in a few ponds. We hoped that providing more specific information on breeding and non-breeding sites would enable Eglin managers to prioritize particular areas for protection. Also, information on the rate of turnover in use of breeding sites by Florida bog frogs, and on movements between sites by both species, could reveal whether these species exhibit metapopulation structure and

need to be managed accordingly. Finally, determining the effect of fire regime on adult flatwoods salamanders might allow managers to prioritize fire management in certain areas.

Objectives
1. To survey known and potential breeding locations of flatwoods salamanders to determine current distribution, population size, and turnover.
2. To obtain baseline information on demography of flatwoods salamanders (annual variation in number of breeding adults, annual variation in larval density, mark-recapture estimates of survival and dispersal) for future use in population models.
3. To compare use by flatwoods salamanders of breeding sites in areas with different disturbance histories, with a focus on fire history.
4. To survey known and potential breeding locations of Florida bog frogs to determine current distribution, population size and turnover, and to quantify habitat characteristics of occupied and unoccupied sites.
5. To mark individual Florida bog frogs to begin collecting information on growth, survival, and dispersal.

Methods
    Much of the work on Florida bog frogs and flatwoods salamanders during the study period was conducted by David Bishop as part of his Ph.D. dissertation research. Many of the results of these studies have already been submitted to Eglin in Dr. Bishop's completed dissertation (Bishop 2005) and other documents (Bishop 2004; Bishop and Haas 2005). Here we provide a summary of this work, reporting full details only for those aspects of the work not previously submitted to Eglin. For additional information, see the documents listed above.

Objectives 1 and 2
    We used information previously collected by Florida Natural Areas Inventory (FNAI) and maps of the base to select study sites for salamanders. We conducted larval surveys in January, February, and March 2002-2005 in wetlands identified by FNAI as active or potential breeding wetlands. Also, we conducted larval surveys during these same periods in wetlands that were not surveyed or mentioned by FNAI, but that we identified as areas of potential habitat. Flatwoods salamanders usually deposit eggs in October and November and hatching usually occurs in December, but is dependent on rains (Means 1972; Anderson and Williamson 1976; Palis 1995), so the months of January through March are generally considered the most effective months for sampling. To find larvae we dipnetted ponds using Model SH-2 and SH-2D (Mid-Lakes Corporation, Knoxville, TN) dipnets and concentrated efforts on areas with inundated herbaceous vegetation. To sample for adults, we constructed partial drift fences at two historic breeding sites (Bishop 2004) following methods described by Palis (1997).
    We originally planned much more extensive drift fence sampling involving complete encircling of 2-6 ponds, as well as extensive roadside surveys in October and November during rains associated with cold fronts when adults would be expected to be traveling to breeding wetlands (Means 1972; Means et al. 1996). However these techniques proved inefficient due to extremely low encounter rates with adult salamanders (see below). Therefore we relied on larval surveys to assess salamander distribution and reproductive activity, and were unable to assess adult demography or population size.

Objective 3

   To assess impacts of fire, we collected data on the burning trends of flatwoods salamander habitat throughout the range of the species, including the fire histories of the 18 historical breeding wetlands on Eglin (Bishop and Haas 2005). We also planned an experimental burn of historic ponds and collected habitat and water chemistry data to evaluate the effects of burning.

Objective 4

   We surveyed sites identified by FNAI for calling adults from April-August 2002-2005. Further, we surveyed additional sites in habitat similar to previously identified sites ("shallow, non-stagnant acid (pH 4.1-5.5) seeps and along shallow, boggy overflows . . . [associated with small clear streams that] drain extensive uplands of deep, excessively drained, sandy soils of the Lakeland-Troup series" (Moler 1985)) for calling adults from May-August. We had hoped to employ tadpole surveys as an additional means to assess distribution, but it proved too difficult to differentiate between small Florida bog frog and bronze frog (*Rana clamitans*) tadpoles to rely on this technique.

   We originally planned to quantify habitat characteristics (pH, water temperature, flow rate, connectivity with other bodies of water, vegetation immediately surrounding site) of surveyed sites in order to compare occupied and unoccupied sites, and thereby better specify the habitat requirements of the species. However, we decided to defer this aspect of the study in order to increase emphasis on Objective 5, which proved surprisingly conducive to study. Habitat selection by Florida bog frogs is a major component of the dissertation research of Tom Gorman, who joined our research team in August 2005. We will report on habitat selection and other aspects of Mr. Gorman's work in future years.

Objective 5

   Work on this objective was expanded to become the primary focus of Dr. Bishop's research, accounting for five of the six chapters of his dissertation. Complete methods relating to this objective are described in Bishop (2005).

Results and Discussion

Flatwoods Salamanders

   We conducted 275 surveys for flatwoods salamanders during 2002-2005, including visits to dry sites and dipnetting and drift fencing at sites with water. The majority of these surveys were dipnet surveys for larval salamanders, but three adults were captured using partial drift fences in 2002. Surveys were conducted at 105 of the 110 wetlands on Eglin considered to have some potential as breeding sites. We determined that 58 of these sites have little to no potential as breeding ponds because the wetlands are too ephemeral or are surrounded by habitat that is too xeric. Additional details about survey efforts are provided in Bishop (2004).

   Prior to this study flatwoods salamanders had been documented in 17 wetlands on Eglin (Palis and Jensen 1995). We detected salamanders at six of these historic breeding locations during our study, and at one new breeding location. Larval salamanders were found at six of these sites, and at the seventh site two adults were captured, but no larvae were detected (Table 18). Many of the 17 historic sites never contained sufficient water to be sampled during the study period. Thus, although flatwoods salamanders have now been captured at 18 different wetlands on Eglin, they have not been recorded at several of these sites for over a decade.

Table 18. Captures of flatwoods salamanders on Eglin (2002–2005). Site ID corresponds to the numbering system of Bishop (2004) and Survey ID corresponds to the survey record in the salamander database.

Site ID	Date	Type of Survey	Survey ID	Captures
2	28-Oct-02	Drift Fence	180	1 Adult Female
	19-Jan-04	Dipnet	281	3 Larvae
	3-Mar-04	Dipnet	355	2 Larvae
30	31-Oct-02	Drift Fence	228	1 Adult Female
	13-Dec-02	Drift Fence	251	1 Adult Male
36	19-Jan-04	Dipnet	283	4 Larvae
	4-Feb-04	Dipnet	312	2 Larvae
	3-Mar-04	Dipnet	356	1 Larva
4	19-Jan-04	Dipnet	277	5 Larvae
	2-Mar-04	Dipnet	312	1 Larva
	16-Feb-05	Dipnet	375	1 Larva
5	17-Jan-03	Dipnet	213	1 Larva
	19-Jan-04	Dipnet	276	4 Larvae
	2-Mar-04	Dipnet	348	3 Larvae
	23-Jan-05	Dipnet	387	4 Larvae
	16-Feb-05	Dipnet	374	1 Larva
15	21-Jan-04	Dipnet	290	1 Larva
	1-Mar-04	Dipnet	345	1 Larva
53	22-Jan-04	Dipnet	298	3 Larvae
	2-Mar-04	Dipnet	349	2 Larvae
	23-Jan-05	Dipnet	396	1 Larva

We detected salamanders at three sites in the 2003 breeding season, six in 2004, and three in 2005. At only one location were salamanders detected in all three years, and they were detected in only one year at three of the seven sites. Four of the wetlands where we captured larvae in 2004 dried in late March, and the single wetland where we captured larvae in 2003 (see Table 18) dried in February. The larval period of *A. cingulatum* is 11–18 weeks, with individuals metamorphosing around 39–43 mm snout–vent length (Palis 1995). Based on the size of the larvae captured in these wetlands, their estimated growth rates (1.7–2.5 mm/week, Palis 1995), and the timing of the dry–down, it is unlikely these individuals survived to metamorphosis. Thus, there likely was little population recruitment over the last few years, even from the few wetlands where larvae were detected.

Detection of larvae and adults is difficult, so lack of detection is not a definite indicator of absence from a location. Still, we conclude that successful reproduction was limited to a handful

of wetlands during the study period, that breeding flatwoods salamanders were neither abundant nor widely distributed on the base, and that breeding activity was considerably reduced compared to the original surveys in 1993 and 1994. The decrease in the numbers of individuals and active breeding wetlands detected may be due, in part, to several years of drought in the late 1990s and early 2000s in northwest Florida. Rainfall needs to be sufficient to fill wetlands and maintain hydroperiods long enough for larvae to complete metamorphosis. It is difficult to determine the extent to which our observations indicate a population decline rather than reduced activity due to poor breeding conditions, as no long–term datasets exist for *A. cingulatum* that would enable one to understand natural population fluctuations. Eglin and other locations should continue annual monitoring programs and combine efforts to try and predict how weather patterns and land–use modifications affect flatwoods salamander population dynamics. See Bishop (2004) for additional data and discussion related to salamander surveys.

We did not collect demographic data to address objective 2. Because of the large effort required and the apparent low population levels, in concert with Jackson Guard staff we decided against extensive drift fence work. Monitoring of historic breeding wetlands was more successfully done using dipnetting, but dipnetting provides limited information about population demography. To calculate relative abundance estimates based on dipnetting we would have had to expend much greater effort dipnetting in each pond, which could potentially disturb the population significantly. Lacking evidence of how disruptive intensive dipnetting would be, we suggest that simply looking at occupancy over time would be a more appropriate, although admittedly very crude, means of tracking population trends.

The planned experimental burn treatment was never implemented, but we were able to assess effects of fire on wetlands used by flatwoods salamanders by collecting data on water chemistry and habitat characteristics of ponds and relating these features to burn history. This work comprised a chapter (Chapter 6) of David Bishop's dissertation, which was subsequently published (Bishop and Haas 2005). See Bishop (2005) and Bishop and Haas (2005) for complete results and discussion. Briefly, we analyzed 13 breeding wetlands on Eglin and found that recently burned wetlands had more open canopies, higher dissolved oxygen concentrations, higher water temperatures, more understory vegetation, and lower water depths than unburned areas. These impacts of burning likely have a positive influence on salamander reproduction. We suggest that more frequent burning of wetlands used by salamanders, particularly growing season burning, would improve conditions for the salamanders. Recent publications on amphibian response to burning support the idea that growing-season burns, or fires that burn through the wetlands, are important for maintaining high-quality breeding habitat for flatwoods salamanders (Russell et al. 1999, Pilliod et al. 2003, Schurbon and Fauth 2003, Means et al. 2004). Our range-wide analysis of 154 breeding wetlands revealed an average fire return interval of 4.4 years (SD = 2.9 years), with fires being three times more likely to occur during the winter (December to April) than in the summer (May-August). This suggests that lack of growing season fire in breeding wetlands is a range-wide problem.

Florida Bog Frogs

Florida bog frogs were first located in 1982 and described as a species in 1985 (Moler 1985). Subsequently 1,327 surveys have been conducted, 1,049 of these by us as part of this study. This survey effort has resulted in the documented presence of Florida bog frogs in a total of 66 locations (Table 19; Figure 25). Six additional locations were first documented by volunteers, but we never detected bog frogs at these locations, and therefore consider them

unconfirmed sites. Of the 66 confirmed sites, 37 were located and frog presence was determined before 2002. During 2002-2005 we located 29 new sites. These new sites are located (up or downstream) in previously documented drainages.

Table 19. Survey histories of 66 confirmed Florida bog frog sites from 1982-2005. 1 = confirmed presence during time period, 0 = no frogs detected during time period, and * = no surveys conducted during time period.

			Year			
Site ID	1982-1991	1991-2001	2002	2003	2004	2005
1	1	0	*	0	0	0
2	1	1	0	0	1	1
3	1	1	1	1	1	1
4	1	1	1	1	1	0
5	1	1	1	1	1	0
6	1	1	*	0	0	0
7	0	1	*	*	1	*
8	1	1	*	0	0	0
9	1	0	*	0	0	0
10	1	0	*	0	0	0
11	1	0	0	0	0	0
12	1	1	*	0	0	1
13	*	1	0	1	1	0
14	*	1	1	1	1	1
15	1	1	*	*	1	*
16	*	1	0	1	1	0
17	*	1	*	1	1	1
18	*	1	*	*	0	1
19	*	1	*	*	1	*
20	*	1	*	1	1	1
21	*	1	*	1	1	1
22	*	0	*	*	1	*
23	*	1	*	*	*	*
24	*	1	*	1	1	1
25	*	1	*	*	1	*
26	*	1	*	1	1	1
27	*	1	*	0	0	*
28	1	1	*	*	0	1
29	1	1	*	0	0	1
32	*	0	1	0	1	1
34	1	1	1	1	1	1
39	*	1	0	0	0	0
42	*	*	0	1	0	0
51	*	1	*	*	1	1
52	*	0	*	0	0	1
56	*	0	*	1	0	0
77	*	1	*	0	0	*

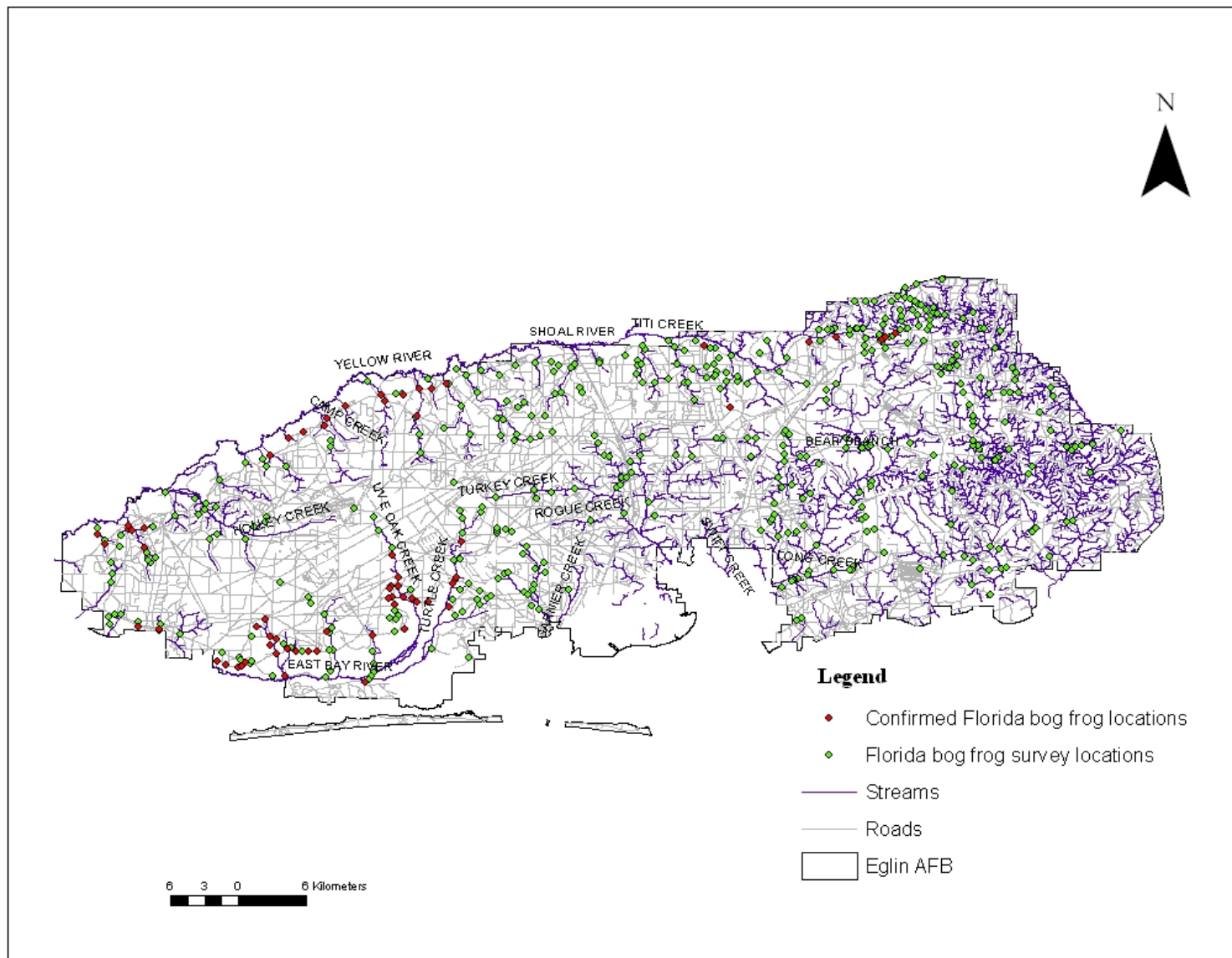|						
78	*	1	*	0	0	*
84	*	1	0	0	0	0
86	*	*	0	1	1	*
105	*	*	1	0	0	*
125	*	*	1	1	1	1
150	*	*	0	1	1	*
160	1	*	*	0	0	0
161	1	*	*	0	0	*
162	*	*	*	*	1	*
163	*	*	*	1	1	1
170	*	*	*	1	1	*
173	*	*	*	1	0	*
177	*	*	*	1	0	*
183	*	*	*	1	0	0
185	*	*	*	1	1	*
187	*	*	*	1	0	*
192	*	1	*	0	0	*
211	*	*	*	1	1	1
212	*	*	*	*	1	1
226	*	*	*	1	0	0
247	*	*	*	*	1	*
266	*	*	*	*	1	*
298	*	*	*	*	1	*
400	*	*	*	*	1	*
472	*	*	*	*	1	*
482	*	*	*	*	1	*
483	*	*	*	*	1	*
488	*	*	*	*	1	*
489	*	*	*	*	*	1

Figure 25. Survey locations and confirmed Florida bog frog sites on Eglin Air Force Base, 2002-2005.

Our survey effort was primarily focused on documenting distribution, so we did not visit every site every year. Of the 37 historic sites, 23 were active during at least one year from 2002-2005, and the other 14 sites had no confirmed presence during 2002-2005 based on surveys in two (n=5), three (n=6) or four (n=3) years (Table 19). Among the historic sites that were still active, we detected frogs in 78% of the visits, which is similar to the detection rate (69%) among the 29 newly documented sites. Thus the probability that frogs could by chance be missed in an occupied site four times (24%) or even three times (34%) is fairly low, suggesting that some historic sites are no longer used by the frogs. We surveyed 14 sites every year of the study (2002-2005) and 33 sites the last three years (2003-2005). The proportion of these sites at which presence of bog frogs was documented in any given year varied relatively little (50%-58%) (Figure 26). Although the proportion of these sites at which frogs were detected declined slightly over the last three years of the study (Figure 26), the data are best interpreted as indicative of a stable population.
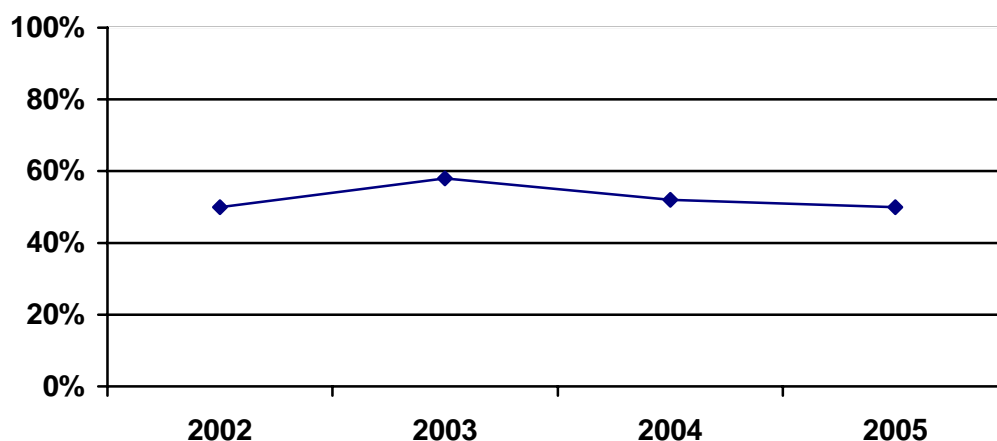

Figure 26. The proportion of Florida bog frog sites surveyed annually at which calling adults were detected. N=14 for 2002, and 33 for 2003-2005.

Some of the variability in site occupancy is undoubtedly due to failure to detect frogs when they actually were present. Repeated visits to sites within a year revealed that the probability of detecting frogs in a single visit in a site occupied by bog frogs averaged about 66%. Probability of detection varied among nights because bog frogs were less likely to call at cool temperatures and early in the season (Figure 27). We therefore recommend that surveys should not be conducted before 1 May, and that a minimum temperature threshold for surveying should be established. To track population trends, we recommend focusing on a subset of sites and visiting these repeatedly each year, rather than trying to survey all sites each year.

Although failure to detect frogs that were actually present may account for the absence of frogs from some sites in our data, it is clear that the frogs do disappear from some previously occupied sites. It may also be that the frogs reoccupy previously abandoned sites and colonize new sites, but we cannot address this with our data because we did not visit sites often enough to determine presence/absence with certainty. Patterns of abandonment, reoccupation and colonization should become clearer once a standardized monitoring protocol is established and applied for a number of years. A likely possibility is that such patterns are related to habitat

needs and changes in habitat condition over time, with frogs abandoning sites as habitat becomes unsuitable and colonizing newly created areas of suitable habitat.
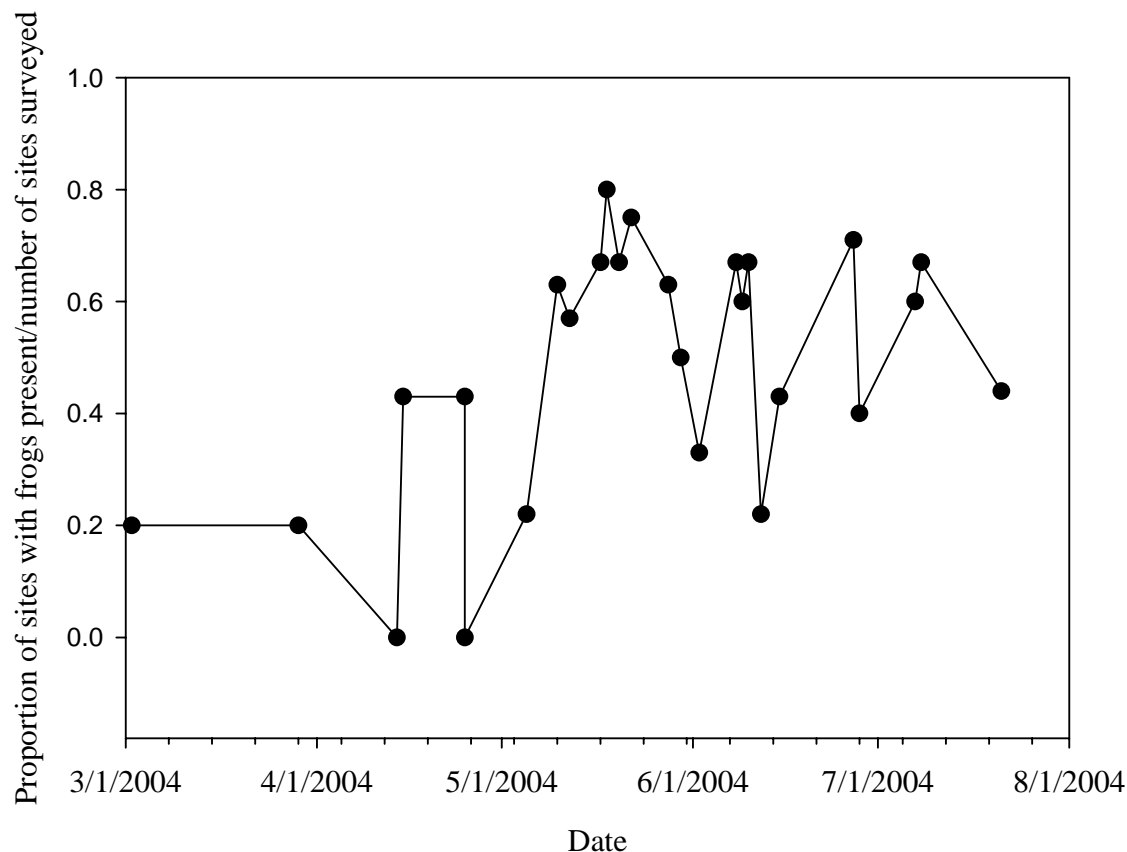

Figure 27. The proportion of sites where bog frogs were documented per total number of sites surveyed that night. All sites included in this analysis were known to have bog frogs present.

The general features of Florida bog frog habitat are now clear. The frogs occur in several different aquatic habitats, including the bends of streams, overflow areas adjacent to streams, the headwaters of streams, isolated seepages, areas downstream of impoundments, and occasionally the edges of ponds above impoundments. Within each of these habitats, individuals select shallow, low–flowing sites, typically near emergent structure (e.g. vegetation, woody debris) and cover. (Further details about microhabitats used by bog frogs at one site may be found in Bishop 2005). Within occupied drainages on Eglin, there are distinct gaps in the distribution of bog frogs (Figure 25). Surveys have been conducted in most of the uninhabited streams, suggesting that if bog frogs actually are present, they are low in abundance or are geographically restricted. The interconnectedness of the streams suggests that tadpoles or adults could access other tributaries in the same drainage. In many cases the general habitat characteristics of surveyed locations in unoccupied streams are not noticeably different from occupied sites in other drainages. However, we did not examine habitat in sufficient detail on the broad spatial scale required to determine the extent to which habitat features can account for frog distribution. This will be a primary objective of subsequent work being conducted by Tom Gorman.

It may be that bog frog distribution is limited not only by habitat requirements, but also by dispersal behavior and metapopulation dynamics. That is, the frogs may be absent from suitable

habitat in some locations because individuals are unable to access those locations through dispersal from existing populations, or because local populations cycle through periods of extinction and recolonization. Dispersal behavior and metapopulation dynamics are additional aspects of bog frog biology we will pursue in subsequent research. The issue of limitation by habitat versus movement and metapopulation dynamics applies to distribution patterns between, as well as within, drainages. On Eglin the frogs are restricted to tributaries of the Yellow, Shoal, and East Bay River drainages in the northern and southwestern portions of the base, and are absent from drainages in the south-central and eastern portions (Figure 25). The extensive stream and seepage slope system in the eastern half of the base in particular appears to provide suitable microhabitat for *R. okaloosae*, although many of the streams on the east side of Eglin are more ephemeral than streams on the west side. It may be that bog frogs inhabit these drainages at times, but are more prone to extinction of local populations there. We intend to examine the role that habitat requirements, dispersal and metapopulation dynamics play in determining distribution on this scale, as well as within drainages, in our subsequent work.

The behavior, population biology and vocalizations of the Florida bog frog were the focus of David Bishop's dissertation. We will not present this work in full here, but will instead summarize the major results. See Bishop (2005) for additional details.

Bishop's study involved intensive monitoring of a population at one site for three breeding seasons. Population size at this site varied among years, and about 20% of the individuals present in one year returned to the site the next year. Females laid eggs from March to August, with a mean clutch size of 235 eggs. Eggs were deposited close to male calling locations, suggesting that males choose calling sites that are suitable for oviposition. Occasionally there were satellite males associated with calling males. Male mating success was correlated with the number of nights a male spent calling, but not body size. Males produced a response call during the vocalizations of other males, which is unusual, as frogs typically avoid acoustical interference, which disrupts the orientation and recognition ability of females. Males typically called in the same location for several days or weeks, but these stationary movements were separated by movements to other locations. Within a season male home range size averaged $188m^2$ (95% fixed kernel), and males moved an average of 22m linear distance along the stream.

The spatial distribution of Florida bog frogs relative to bronze frogs inhabiting the same streams indicated potential for competition between the two species. The calls of the two species are distinguishable, but bog frogs react to bronze frog calls, albeit not as strongly as to conspecific calls. Occasional hybridization between the species is likely. The calls of individual bog frogs are somewhat distinguishable, but not sufficiently so to employ individual voice recognition as a means to measure population size.

Overall the results suggest that Florida bog frogs have a complex mating system, with local populations consisting of territorial calling males that sometimes have satellite males associated with them. The interaction of bog frogs with bronze frogs, behaviorally, ecologically and evolutionarily, emerged from this work as an interesting issue, and as an additional factor that may limit the distribution of the Florida bog frog.

GRADUATE STUDENT TRAINING

The project provided funding for two graduate students. One position was occupied by Ms. Lori Blanc, who began her degree program at the outset of the project in January 2001. Thus Ms. Blanc received five years of funding, during which time she conducted the work on the

cavity-nesting bird community reported here. She will complete her dissertation in May 2007, and will submit it to Eglin as an additional product of this project at that time.

The second position initially was occupied by David Bishop, starting in August 2001 when he began his degree program. Dr. Bishop conducted the work on flatwoods salamanders and Florida bog frogs reported here. He received four years of funding, and completed his dissertation in June 2005. This dissertation has been submitted to Eglin as an additional product of the project. Following Dr. Bishop's graduation, the second position was occupied by Mr. Tom Gorman for one semester at the end of the project (August – December 2005). Mr. Gorman is continuing the work on salamanders and frogs begun by Dr. Bishop.

LITERATURE CITED

Allen, D. H. 1991. An insert technique for constructing artificial red-cockaded woodpecker cavities. USDA Forest Service General Technical Report SE-73.

Allen, D. H., K. E. Franzreb and R. F. Escano. 1993. Efficacy of translocation strategies for red-cockaded woodpeckers. Wildlife Society Bulletin 21:155-159.

Allen, J. C., S. M. Krieger, J. R. Walters and J. A. Collazo. 2006. Associations of breeding birds with fire-influenced and riparian-upland gradients in a longleaf pine ecosystem. Auk 123. In press.

Anderson, J. D. and G. K. Williamson. 1976. Terrestrial mode of reproduction in *Ambystoma cingulatum*. Herpetologica 32:214-221.

Angelstam, P. 1990. Factors determining the composition and persistence of local woodpecker assemblages in taiga forest in Sweden – A case for landscape ecological studies. In Conservation and Management of Woodpecker Populations (A. Carlson and G. Aulen, eds.). Uppsala, Sweden: Swedish University of Agricultural Sciences, Department of Wildlife Ecology Report 17.

Ash, A. 1988. Disappearance of salamanders from clearcut plots. Journal of the Elisha Mitchell Scientific Society 104:116-122.

Ash, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conservation Biology 11:983-989.

Ashton, R. E., Jr. 1992. Flatwoods salamander *Ambystoma cingulatum* (Cope). Pages 39-43 in Rare and Endangered Biota of Florida: Reptiles and Amphibians (P.E. Moler, ed.). Gainesville, FL: University Press of Florida.

Bennett, S. H., J. W. Gibbons and J. Glanville. 1980. Terrestrial activity, abundance, and diversity of amphibians in differently managed forest types. American Midland Naturalist 103 412-416.

Bibby, C. J., N. D. Burgess and D. A. Hill. 1992. Bird census techniques. San Diego, CA: Academic Press.

Bishop, D. C. 2004. Summary of surveys for Florida bog frogs and flatwoods salamanders on Eglin Air Force Base through 2004. Blacksburg, VA: Virginia Tech University.

Bishop, D. C. 2005. Ecology and distribution of the Florida bog frog and flatwoods salamander on Eglin Air Force Base. PhD Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Bishop, D. C., and C. A. Haas. 2005. Burning trends and potential negative effects of suppressing wetland fires on flatwoods salamanders. Natural Areas Journal 25:290-294.

Brown, C. R. 1997. Purple Martin (*Progne subis*). In The Birds of North America, No. 287 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Burton, T. M. and G. E. Likens. 1975a. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 56:1068-1080.

Burton, T. M. and G. E. Likens. 1975b. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975:541-546.

Carter, J. H., III, J. R. Walters, S. H. Everhart and P. D. Doerr. 1989. Restrictors for red-cockaded woodpecker cavities. Wildlife Society Bulletin 17:68-72.

Chazal, A. C. and P. H. Niewiarowski. 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. Ecological Applications 8:1133-1143.

Cohen, J. E., F. Briand and C. M. Newman. 1990. Community Food-webs: Theory and Data. London: Springer-Verlag.

Conner, R. N. and D. C. Rudolph. 1995. Excavation dynamics and use patterns of red-cockaded woodpecker cavities: Relationships with cooperative breeding. Pages 343-352 in Red-cockaded Woodpecker: Recovery, Ecology and Management (D. L. Kulhavy, R. G. Hooper and R. Costa, eds.). Nacogdoches, TX: College of Forestry, Stephen F. Austin State University.

Conner, R. N., D. C. Rudolph and J. R. Walters. 2001. The Red-cockaded Woodpecker: Surviving in a Fire-Maintained Ecosystem. Austin, TX: University of Texas Press.

Convery, K. M. 2002. Assessing habitat quality for the endangered red-cockaded woodpecker (*Picoides borealis*). M.S. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Copeyon, C. K. 1990. A technique for constructing cavities for the red-cockaded woodpecker. Wildlife Society Bulletin 18:303-311.

Copeyon, C. K., J. R. Walters and J. H. Carter, III. 1991. Induction of red-cockaded woodpecker group formation by artificial cavity construction. Journal of Wildlife Management 55:549-556.

Costa, R. 1995. Red-cockaded woodpecker recovery on private lands: a conservation strategy responsive to the issues. Pages 67-74 in Red-cockaded Woodpecker: Recovery, Ecology and Management (D. L. Kulhavy, R. G. Hooper and R. Costa, eds.). Nacogdoches, TX: College of Forestry, Stephen F. Austin State University.

Costa, R. 2004. State of the red-cockaded woodpecker world: highlights of the previous decade (1992-2002). Pages 39-46 in Red-cockaded Woodpecker: Road to Recovery (R. Costa and S. J. Daniels, eds.). Blaine, WA: Hancock House Publishing.

Costa, R. and S. J. Daniels (eds.). 2004. Red-cockaded Woodpecker: Road to Recovery. Blaine, WA: Hancock House Publishing.

Crowder, L. B., J. A. Priddy and J. R. Walters. 2000. Dynamics of red-cockaded woodpecker populations at Eglin Air Force Base, Blackwater River State Forest and Conecuh National Forest: A model analysis. Blacksburg, VA: Virginia Tech University.

DeFazio, J. T., Jr., M. A. Hunnicutt, M. R. Lennartz, G. L. Chapman and J. A. Jackson. 1987. Red-cockaded woodpecker translocation experiments in South Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 41:311-317.

DeMaynadier, P. G. and M. L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12:340-352.

Department of Defense - Air Force. 1999. Integrated Natural Resources Transitional Plan, Eglin Air Force Base, Florida. Niceville, FL: Natural Resources Management Branch, Eglin Air Force Base.

de Ruiter, P. C., A.-M. Neutel and J. C. Moore. 1995. Energetics, patterns of interaction strengths and stability in real ecosystems. Science 269:1257-1260.

Dobkin, D. S., A. C. Rich, J. A. Pretare and W. H. Pyle. 1995. Nest-site relationships among cavity-nesting birds in south central British Columbia. Canadian Journal of Zoology 67:1067-1073.

Doerr, P. D., J. R. Walters and J. H. Carter, III. 1989. Reoccupation of abandoned clusters of cavity trees (colonies) by red-cockaded woodpeckers. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 43:326-336.

Edwards, J. W. and R. Costa. 2004. Rangewide success of red-cockaded woodpecker translocation. Pages 307-311 in Red-cockaded Woodpecker: Road to Recovery (R. Costa and S. J. Daniels, eds.). Blaine, WA: Hancock House Publishing.

Everhart, S. H., P. D. Doerr and J. R. Walters. 1993. Snag density and interspecific use of red-cockaded woodpecker cavities. Journal of the Elisha Mitchell Scientific Society 109:37-44.

Florida Fish and Wildlife Conservation Commission. 1997. Florida's endangered species, threatened species, and species of special concern: official lists. Tallahassee, FL: Florida Fish and Wildlife Conservation Commission.

Franzreb, K. E. 1997. Success of intensive management of a critically imperiled population of red-cockaded woodpeckers in South Carolina. Journal of Field Ornithology 68:458-470.

Frost, C. C., J. Walker and R. K. Peet. 1986. Fire-dependent savannas and prairies of the southeast: original extent, preservation status and management. Pages 348-357 in Wilderness and Natural Areas in the Eastern United States: A Management Challenge (D. L. Kulhavy and R. N. Connor, eds.). Nacogdoches, TX: Stephen F. Austin State University.

Gault, K. E., J. R. Walters, J. Tomcho, Jr., L. F. Phillips, Jr. and A. Butler. 2004. Nest success of Southeastern American Kestrels associated with Red-cockaded Woodpeckers in old-growth longleaf pine habitat in Northwest Florida. Southeastern Naturalist 3:191-204.

Gibbs, J .P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13:263-268.

Grialou, J. A., S. D. West and R. N. Wilkins. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. Journal of Wildlife Management 64:105-113.

Halliday, T. 1998. A declining amphibian conundrum. Nature 394:418-419.

Hanlin, H. G., F. D. Martin, L. D. Wike and S. H. Bennett. 2000. Terrestrial activity, abundance and species richness of amphibians in managed forests in South Carolina. American Midland Naturalist 143:70-88.

Hardesty J. L., K. E. Gault and H. F. Percival. 1997. Ecological correlates of red-cockaded woodpecker (*Picoides borealis*) foraging preference, habitat use and home range size in northwest Florida (Eglin Air Force Base). Final Report, Research Work Order 99. Gainesville, FL: University of Florida.

Harding, S. R. and J. R. Walters. 2002. Processes regulating the population dynamics of red-cockaded woodpecker cavities. Journal of Wildlife Management 66:1083-1095.

Harding, S. R. and J. R. Walters. 2004. Dynamics of cavity excavation by red-cockaded woodpeckers. Pages 412-422 in Red-cockaded Woodpecker: Road to Recovery (R. Costa and S. J. Daniels, eds). Blaine, WA: Hancock House Publishing.

Harpole, D. N. and C. A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management 114:349-356.

Herbeck, L. A. and D. R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. Conservation Biology 13:623-632.

Hoffman, M. L., and M. W. Collopy. 1988. Historical status of the American Kestrel (*Falco sparverius paulus*) in Florida. Wilson Bulletin 100:91-107.

Hooper, R. G. 1983. Colony formation by red-cockaded woodpeckers: hypotheses and management implications. Pages 72-77 in Red-cockaded Woodpecker Symposium II (D. A. Wood, ed.). Atlanta, GA: Florida Game and Freshwater Fisheries Commission, U. S. Fish and Wildlife Service.

Hooper, R. G., D. L. Krusac and D. L. Carlson. 1991. An increase in a population of red-cockaded woodpeckers. Wildlife Society Bulletin 19:277-286.

Hooper, R. G., W. E. Taylor and S. C. Loeb. 2004. Long-term efficacy of artificial cavities for red-cockaded woodpeckers: Lessons learned from Hurricane Hugo. Pages 430-438 in Red-cockaded Woodpecker: Road to Recovery (R. Costa and S. J. Daniels, eds). Blaine, WA: Hancock House Publishing.

Hutto, R. L., S. M. Pletschet and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593-602.

Jackson, J. A. 1994. Red-cockaded woodpecker (*Picoides borealis*). In The Birds of North America, No. 85 (A. Poole and F. Gill, eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Jackson, J. A., M. R. Lennartz and R. G. Hooper. 1979. Tree age and cavity initiation by red-cockaded woodpeckers. Journal of Forestry 77:102-103.

James, F. C., C. A. Hess and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecological Applications 7:118-129.

James, F. C., C. A. Hess, B. C. Kicklighter and R. A. Thum. 2001. Ecosystem management and the niche gestalt of the red-cockaded woodpecker in longleaf pine forests. Ecological Applications 11:854-870.

Kappes, J. J., Jr. 1997. Defining cavity-associated interactions between red-cockaded woodpeckers and other cavity-dependent species: interspecific competition or cavity kleptoparasitism? Auk 114:778-780.

Kappes, J. J. 2004. Species interactions associated with red-cockaded woodpecker cavities at two forests in northern peninsular Florida. Ph.D. Dissertation, University of Florida, Gainesville, FL.

Kappes, J. J. and L. D. Harris. 1995. Interspecific competition for red-cockaded woodpecker cavities in Apalachicola National Forest. Pages 389-393 in Red-cockaded Woodpecker: Recovery, Ecology and Management (D. L. Kulhavy, R. G. Hooper and R. Costa, eds). Nacogdoches, TX: Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State University.

Khan, M. Z. and J. R. Walters. 2002. Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). Behavioral Ecology and Sociobiology 51:336-344.

Kulhavy, D. L., R. G. Hooper and R. Costa (eds.). 1995. Red-cockaded Woodpecker: Recovery, Ecology and Management. Nacogdoches, TX: College of Forestry, Stephen F. Austin State University.

Letcher, B. H., J. A. Priddy, J. R. Walters and L. B. Crowder. 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. Biological Conservation 86:1-14.

Martin, K. and J. M. Eadie. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115:243-257.

Martin, K., K. E. H. Aitken and K. L. Weibe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. Condor 106: 5-19.

Martin, T. E. 1997. Bbird Field Protocol. Missoula, MT: Montana Cooperative Wildlife Research Unit, University of Montana.

McComb, W. C., S. A. Bonney, R. M. Sheffield and N. D. Cost. 1986. Snag resources in Florida- are they sufficient for average populations of primary cavity-nesters? Wildlife Society Bulletin 14:40-48.

McFarlane, R. W. 1973. Florida's sparrow hawk. Florida Field Naturalist 46:20-22.

McFarlane, R. W. 1992. A Stillness in the Pines. New York, NY: W. W. Norton.

Means, D. B. 1972. Notes on the autumn breeding biology of *Ambystoma cingulatum* (Cope) (Amphibia: Urodela: Ambystomatidae). Association of Southeastern Biologists Bulletin 19:84.

Means, D. B., J. G. Palis and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology 10:426-437.

Means, D. B., C. K. Dodd, Jr., S. A. Johnson and J. G. Palis. 2004. Amphibians and fire in longleaf pine ecosystems: response to Schurbon and Fauth. Conservation Biology 18:1149-1153.

Moler, P. E. 1985. A new species of frog (Ranidae: *Rana*) from northwestern Florida. Copeia 1985: 379-383.

Moler, P. E. 1993. *Rana okaloosae*. Catalogue of American Amphibians and Reptiles: 561.1-561.3.

Moore, W. S. 1995. Northern Flicker (Colaptes auratus). In The Birds of North America, No. 166 (A. Poole and F. Gill, eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Palis, J. G. 1995. Larval growth, development, and metamorphosis of *Ambystoma cingulatum* on the Gulf Coastal Plain of Florida. Florida Scientist 58:352-358.

Palis, J. G. 1996. Flatwoods salamander (*Ambystoma cingulatum* Cope). Natural Areas Journal 16:49-54.

Palis, J. G. 1997. Breeding migration of Ambystoma cingulatum in Florida. Journal of Herpetology 31:71-78.

Palis, J. G. and J. B. Jensen. 1995. Distribution and breeding biology of the flatwoods salamander (*Ambystoma cingulatum*) and gopher frog (*Rana capito*) on Eglin Air Force Base, Florida. Final Report. Tallahassee, FL: Florida Natural Areas Inventory.

Pechmann, J. H. K. and H. M. Wilbur. 1994. Putting declining amphibian populations into perspective: natural fluctuations and human impacts. Herpetologica 50:65-84.

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Petranka, J. W., M. E. Eldridge and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7:363-370.

Petranka, J. W., M. P. Brannon, M. E. Hopey and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67:135-147.

Pilliod, D. S., R. B. Bury, E. J. Hyde, C. A. Pearl and P. S. Corn. 2003. Fire and amphibians in North America. Forest Ecology and Management 178:163-181.

Pimm, S. L. 1980. Properties of food webs. Ecology 61:219-225.

Pough, F. H., E. M. Smith, D. H. Rhodes and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management 20:1-9.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609-620.

Provencher L. A., R. Litt, K. E. M. Galley, D. R. Gordon, G. W. Tanner, N. M. Gobris, S. J. McAdoo, J. P. McAdoo and B. J. Herring. 2001. Restoration of fire-suppressed longleaf pine sandhills at Eglin Air Force Base, Florida. Final report to the Natural Resource Management Division, Eglin Air Force Base, Niceville, Florida. Gainesville, FL: Science Division, The Nature Conservancy.

Provencher, L., N. M. Gobris, L. A. Brennan, D. R. Gordon, and J. L. Hardesty. 2002. Breeding bird response to midstory hardwood reduction in Florida sandhill longleaf pine forests. Journal of Wildlife Management 66:641-661.

Rudolph, D. C., R. N. Conner and J. Turner. 1990. Competition for Red-cockaded Woodpecker roost and nest cavities: Effects of tree age and entrance diameters. Wilson Bulletin 102:23-36.

Rudolph, D. C., R. N. Conner, D. K. Carrie and R. R. Shaefer. 1992. Experimental reintroduction of red-cockaded woodpeckers. Auk 109:914-916.

Rudolph, D. C., R. N. Conner and J. R. Walters. 2004. Red-cockaded woodpecker recovery: an integrated strategy. Pages 70-76 in Red-cockaded Woodpecker: Road to Recovery (R. Costa, and S. J. Daniels, eds.). Blaine, WA: Hancock House Publishing.

Russell, K. R., D. H. Van Lear and D. C. Guynn, Jr. 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin 27:374-384.

Saab, V. A., J. Dudley and W. L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106:20-36.

Saenz, D., R. N. Conner, C. E. Shackelford and D. C. Rudolph. 1998. Pileated Woodpecker damage to Red-cockaded Woodpecker cavity trees in eastern Texas. Wilson Bulletin 110:362-367.

Schurbon, J. M. and J. E. Fauth. 2003. Effects of prescribed burning on amphibian diversity in a southeastern U.S. National Forest. Conservation Biology 17:1338-1349.

Sedgwick, J. A. 1997. Sequential cavity use in a cottonwood bottomland. Condor 99:880-887.

Thompson, R. L. (ed.). 1971. The Ecology and Management of the Red-cockaded Woodpecker. Tallahassee, FL: Bureau of Sport Fisheries and Wildlife, U.S. Department of the Interior and Tall Timbers Research Station.

U.S. Fish and Wildlife Service. 2003. Red-cockaded Woodpecker (*Picoides borealis*) Recovery Plan: Second Revision. Atlanta, GA: U.S. Fish and Wildlife Service.

Van Balen, J. H., C. J. H. Booy, J. A. Van Franeker and E. R. Osiek. 1982. Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest sites. Ardea 70:1-24.

Wake, D. B. 1991. Declining amphibian populations. Science 253:860.

Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060-2068.

Walters, E. L. 2004. Estimating species interactions in a woodpecker tree-hole community at the individual, population, and community levels. Ph.D. Dissertation, Florida State University, Tallahassee, FL.

Walters, J. R. 1990. Red-cockaded woodpeckers: a "primitive" cooperative breeder. Pages 67-101 in Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior (P. B. Stacey and W. D. Koenig, eds.). Cambridge: Cambridge University Press.

Walters, J. R. 1991. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. Annual Review of Ecology and Systematics 22:505-523.

Walters, J. R. 2004. Unusual dynamics in a rapidly increasing population of red-cockaded woodpeckers at Camp Lejeune, North Carolina. Pages 256-267 in Red-cockaded Woodpecker: Road to Recovery (R. Costa and S. J. Daniels, eds). Blaine, WA: Hancock House Publishing.

Walters, J. R., J. H. Carter, III, P. D. Doerr and C. K. Copeyon. 1995. Response to drilled artificial cavities by red-cockaded woodpeckers in the North Carolina Sandhills: 4-year assessment. Pp. 380-384 in Red-cockaded Woodpecker: Recovery, Ecology and Management (D. L. Kulhavy, R. G. Hooper and R. Costa, eds). Nacogdoches, TX: Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State University.

Walters, J. R., C. A. Haas and K. E. Gault. 2002a. Adaptive management of red-cockaded woodpeckers on Eglin Air Force Base, Florida: Experimental study. Project final report. Blacksburg, VA: Virginia Tech University.

Walters, J. R., L. B. Crowder and J. A. Priddy. 2002b. Population viability analysis for red-cockaded woodpeckers using an individual-based model. Ecological Applications 12:249-260.

Walters, J. R., S. J. Daniels, J. H Carter, III and P. D. Doerr. 2002c. Defining quality of red-cockaded woodpecker foraging habitat based on habitat use and fitness. Journal of Wildlife Management 66:1064-1082.

Walters, J. R., K. E. Gault, B. W. Hagedorn, C. J. Petrick, L. F. Phillips. Jr., J. Tomcho, Jr. and A. Butler. 2004. Effectiveness of recruitment clusters and intrapopulation translocation in promoting growth of the red-cockaded woodpecker population on Eglin Air Force Base, Florida. Pages 325-334 in Red-cockaded Woodpecker: Road to Recovery (R. Costa and S. J. Daniels, eds). Blaine, WA: Hancock House Publishing.

Walters, J. R., B. Simmons, C. Nycum and R. Meekins. 2005. The biology and management of the red-cockaded woodpecker on Marine Base Camp Lejeune, North Carolina: Progress toward recovery under the new management plan. Blacksburg, VA: Virginia Tech University.

Waltho, N. and J. Kolasa. 1994. Organization of instabilities in multispecies systems: A test of hierarchy theory. Proceedings of the National Academy of Sciences 91:1682-1685.

Ware, S., C. C. Frost and P. D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. Pages. 447-493 in Biodiversity of the Southeastern United States (W. H. Martin, S. G. Boyce and A. C. Echternect, eds.). New York: John Wiley and Sons, Inc.

Warren, P. H. 1990. Variation in food-web structure: The determinants of connectance. American Naturalist 135:689-700.

Watson, J. C., R. G. Hooper, D. L. Carlson, W. E. Taylor and T. E. Milling. 1995. Restoration of the red-cockaded woodpecker population on the Francis Marion National Forest: Three years post Hugo. Pages 172-182 in Red-cockaded Woodpecker: Recovery, Ecology and Management (D. L. Kulhavy, R. G. Hooper and R. Costa, eds.). Nacogdoches, TX: College of Forestry, Stephen F. Austin State University.

Wood, D. A. (ed.). 1983. Red-cockaded Woodpecker Symposium II. Atlanta: Florida Game and Freshwater Fisheries Commission, U.S. Fish and Wildlife Service.